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A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF *PHYLLANTHUS* *

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PHYLLANTHUS, among the subfamily Phyllanthoideae of the Euphorbiaceae, is at once the largest (650 species) and most diversified genus; it includes plants of a great many types of growth form, such as trees, shrubs, annual and perennial herbs, and floating aquatics. Although a number of species grow in dry habitats, none is at home in extreme deserts, whereas many prefer mesophytic or even hydrophytic environments. These ecological characteristics, and the inability of all except two or three species to endure cool conditions such as those in the eastern temperate United States, limit the distribution of the genus as a whole to those areas where tropical and reasonably humid conditions occur. Within these limits, however, the genus is circumtropical, well represented on all the continents and particularly the island groups lying off-shore.

In common with that of most other large angiospermous genera (those with more than 500 species), the present classification of *Phyllanthus* very inadequately reflects the true relationships between the subgeneric taxa. The difficulties in most of these large genera reside largely in their sheer size; a tremendous bibliographic study must be accomplished by the student before he can undertake biological studies of the organisms concerned.

The situation in *Phyllanthus*, however, differs from that in such genera as *Solanum*, *Eugenia*, and *Carex*, where a relatively stereotyped ground-plan prevails throughout the entire genus. In *Phyllanthus* the difficulties incumbent on the great size of the group are aggravated by the fact that there are profound differences in the vegetative structure, flowers, and fruits. Some of these may be accounted for by the fact that *Phyllanthus* in its current circumscription is not an entirely natural genus; but even after the discordant groups are removed, *Phyllanthus* still remains — when vegetative and reproductive organs are considered together — perhaps the most diversified of all the great genera of the Angiosperms. The investigation of its classification and evolution should be carried out with the view of attempting to explain how this great diversity can be reconciled with the “naturalness” of the greater portion of the genus.

* Studies of the Euphorbiaceae, Phyllanthoideae, III.

The present study of the West Indian species of *Phyllanthus*, which has occupied about four years of work, is intended as the first installment of and theoretical basis for a world-wide monograph of the genus. Analysis of some 3,000 herbarium specimens of West Indian species has been supplemented by the study of specimens of many extra-Caribbean species, as well as by three field trips: to Cuba in 1951 and 1953, and to Jamaica in 1954. Of the ninety-odd species accepted in this treatment, 39 have been seen in the living condition. The lack of field work in Hispaniola has been the most keenly felt deficiency, for the species of sections *Cyclanthera* and *Phyllanthus* on that island cannot be satisfactorily understood from the herbarium specimens at hand. Since it seems impractical, however, to delay publication indefinitely in the hope of improving the treatment of these few species, their critical appraisal will be deferred to a future paper.

The eighty-odd native West Indian species of *Phyllanthus* constitute a fascinating assemblage of forms. Adapted to many different habitats and evidencing origin from various ancestral types, they exemplify well the flourishing of an evolutionarily successful group of angiosperms in the insular environment of the Caribbean. It is the main purpose of this work to attempt to capture on paper something corresponding to the biological reality of these plants as they occur today in populations on the West Indian islands, and to indicate what significance this may have for students of the West Indian flora in particular and the evolution of the angiosperms in general.

The results of these studies on the West Indian species of *Phyllanthus* will be presented in three parts: (1) a general section including historical reviews and observations on morphology and anatomy, (2) a systematic section enumerating and describing the taxa, and (3) a concluding section presenting a synthesis of all the data and discussing geographical distribution and evolution within the genus.

HISTORICAL REVIEW

The summary of the taxonomic history of *Phyllanthus* presented here centers mainly around the development of generic concepts in the subtribe Phyllanthinae as defined by Pax (1890), particularly as this applies to the species represented in the West Indies. In a previous paper (Webster, 1956), the history of *Phyllanthus* as it pertains to the American species described by Linnaeus has been discussed, including many nomenclatural details which will be omitted in the following account.

As will be shown in the section on growth form, most of the genera of the subtribe Phyllanthinae of the Phyllanthaceae share a peculiarity of ramification (viz., phyllanthoid branching) which gives them a similar aspect; only the less-evolved species of *Phyllanthus* itself form an exception. Although a critical understanding of phyllanthoid branching has been surprisingly slow in forming, a crude intuitive awareness of it has, since a few species first became familiar to Western botanists in the latter half of the seventeenth century, resulted in the taxa of the Phyllanthinae being treated

more or less together. In the consideration of the taxonomic history of *Phyllanthus*, therefore, it appears most practical to follow together the development of the morphological and generic concepts.

Because of its tropical and entirely non-European distribution, *Phyllanthus* appears to have been unknown to the classical authors such as Theophrastus and Pliny. Bauhin (1623) listed only a single species which would now be placed in the genus; his *Myrobalanus emblica* became the *Phyllanthus emblica* of Linnaeus. Apparently *P. emblica* was introduced into the Mediterranean area by the Arabs, in whose writings the plant is first mentioned; but for several hundred years it was known only from the fruit, which was a medicinal item.

The scientific literature of *Phyllanthus* begins abruptly in the late seventeenth century with publications by Breynius (1678) and Rheede tot Draakestein (1679), both on plants from India. Breynius's *Frutex indicus baccifer* &c. appears to represent *P. reticulatus* Poir., and Rheede's *Niruri* may be the same species. It is interesting to note that although a number of Phyllanthinae were described in various volumes of Rheede's work, the affinities between the herbaceous and woody species were not recognized. Thus, for example, *P. emblica* L. was called *Nili-camarum* while *P. urinaria* was called *Tsieru-Kirganeli*.

Hermann (1689) and Sloane (1696) opened the study of the New World species with descriptions of two species of sect. *Xylophylla*, which quickly became well-known because of their apparently anomalous production of marginal flowers on the leaves. The significance of Hermann's plant, *Phyllanthos americana planta* &c., is that it was the basis for the name which Linnaeus applied to the entire genus. Commelin (1697) illustrated and described what was probably the same plant as Hermann's; the plate is good and easily recognizable as *P. epiphyllanthus*. Plukenet, in his "Phytographia" (1691-1696) described several species of *Phyllanthus* under various names but contributed nothing significant.

In the early part of the eighteenth century, most of the Phyllanthinae were described under two names: *Niruri* for the groups with branchlets resembling pinnate leaves (including species of *Breynia* and *Sauropus* as well as some of *Phyllanthus*), and *Phyllanthus* for the phylloclade-bearing species of *Phyllanthus* sect. *Xylophylla*. Linnaeus, in the first edition of the "Genera Plantarum" (1737), gave Dillenius the credit for first appreciating the fact that *Niruri* and *Phyllanthus* are congeneric. This insight of Dillenius represented the first important step in the development of the modern concept of the genus. He saw that in both *Niruri* and *Phyllanthus* the flowers were borne on apparent leaves, and that these leaf-like structures were homologous: in *Niruri* the flowers occurring in the axils of the leaflets of a pinnately compound "leaf"; in *Phyllanthus* (sensu Commelin), in notches on the margins of an undivided "leaf." Linnaeus, Dillenius, and their contemporaries all erred, however, in assuming that these homologous flower-bearing structures were leaves. As will be shown later, this pseudo-foliar modification of the branches is one of the most important characters in defining the *Phyllanthus*-complex, even though in the present

interpretation it comes closer to characterizing the entire subtribe *Phyllanthinae* than it does the genus *Phyllanthus* alone.

Linnaeus in the "Hortus Cliffortianus" (1738) included in *Phyllanthus* three species, which became in 1753 *P. epiphyllanthus*, *P. niruri*, and *P. grandifolius*. The inclusion of these three very different plants — a phylloclade-bearing shrub, an herb with phyllanthoid branching, and a tree with non-phyllanthoid branching — thus established the genus at the very beginning as one with great diversity in growth form. The next important modification in the generic concept came in Linnaeus's "Flora Zeylanica" (1747) in which the *Myrobalanus emblica* of Bauhin et al. was for the first time associated with the other species of *Phyllanthus*. In the first edition of the "Species Plantarum" (1753) Linnaeus made no important modification, merely adding one new species, *P. maderaspatensis* L.; although this species belongs to a yet different section from the others, its inclusion caused no important change in generic concept.

Linnaeus's next significant contribution, in the "Mantissa" (1767), was the publication of the new genus *Cicca*, characterized by tetramerous flowers. Although he placed it in the Monoecia Tetrandria, he observed that it was related to *Phyllanthus*. Subsequently, no one has doubted the clear affinity of *Cicca* to the other species of *Phyllanthus*; the only difference of opinion has revolved around whether it merits generic or only sub-generic rank.

Four years later, in the "Mantissa Altera," Linnaeus established another new genus, *Xylophylla*, by splitting off *P. epiphyllanthus* from the other species. The new generic name was derived from the *Xylophyllus ceramica* of Rumphius, which Linnaeus renamed *Xylophylla longifolia*. The Rumphian plant, however, although it furnished the generic name, was poorly known and the genus was definitely based on the treatment of two Jamaican species of *Phyllanthus* by Patrick Browne. As indicated in a recent paper (Webster, 1956), Linnaeus and other writers were misled by Browne's erroneous description into thinking that *Xylophylla* had hermaphrodite flowers. It was purely on the basis of this fallacious character, and not upon the phylloclade-bearing habit, that Linnaeus recognized the genus; Swartz finally equated the genera in his "Flora Indiae Occidentalis" (1800), but together with Poiret (1804) and Willdenow (1809) still regarded the flowers as hermaphrodite. The confusion was at last cleared up in 1824 by Adrien de Jussieu, who retained *Xylophylla* but noted "vix a *Phyllantho* diversum." Since *Xylophylla* was merged with *Phyllanthus* by Baillon (1858) and Mueller Argoviensis (1866), relatively few authors have chosen to take it up as a distinct genus, although L. H. Bailey has recently upheld it in his "Manual of Cultivated Plants."

The most important of the post-Linnaean genera of *Phyllanthinae* is undoubtedly *Glochidion*, established by Forster in 1776. The absence of a disk, the characteristic androecium, and the plurilocular ovary with undivided styles all made this a very distinctive group, and it was generally maintained until Mueller Argoviensis (1865, 1866) merged it with *Phyllanthus*. This interpretation was accepted by Bentham in the "Genera

Plantarum" (1880) but reversed by Hooker in the "Flora of British India" (1887). Hooker's judgment was accepted by Pax (1890) and Pax and Hoffman (1931), as well as by most modern authors. Croizat (1943) has upheld *Glochidion* and remarked that it may be upheld "only with the understanding that its species form a natural group that it is not possible to define with reference to a set of conventional characters." This appears rather too pessimistic, however, as it actually is possible to define *Glochidion* on the basis of characters as satisfactory as any in the Phyllanthoideae.

A. L. de Jussieu, in his "Genera Plantarum" (1789), accepted *Cicca*, *Phyllanthus*, and *Xylophylla*, and added a new genus *Kirganelia* based on a Mauritian plant collected by Commerson. *Kirganelia* was distinguished on the basis of its baccate fruit and androecium of five unequally united stamens; although a distinctive group, it has generally been placed in the subgeneric rank under *Phyllanthus*. Jussieu also suggested that *P. emblica* L. might be put in a distinct genus. This was promptly done by Gaertner (1791), who placed the plant in the new genus *Emblia* as *E. officinalis*.

Olaf Swartz, in a series of publications (1788, 1791, 1800) gave the first critical treatment of the West Indian species, carefully distinguishing the Jamaican species of sect. *Xylophylla* and adding several other species. He furthermore established a new genus *Epistylum*, based on two Jamaican plants, which in more recent times has always been accepted as a section of *Phyllanthus*.

The first publication on the Euphorbiaceae which may be regarded as monographic is Adrien de Jussieu's "De Euphorbiacearum Generibus Tentamen" (1824), where for the first time all the previously published genera are critically compared and described. Jussieu accepted eleven genera of Phyllanthinae: *Epistylum*, *Gynoon*, *Glochidion*, *Anisonema*, *Agyneia*, *Cicca*, *Emblia*, *Kirganelia*, *Phyllanthus*, *Xylophylla*, and *Menarda*. This suggests an excessively narrow generic concept, but Jussieu indicates in parenthetical comments that one could just as well unite with *Phyllanthus* half of these genera: *Xylophylla*, *Emblia*, *Kirganelia*, *Cicca*, *Menarda*, and *Agyneia*. The resulting classification, with the exceptions of the inclusion of *Agyneia* in *Phyllanthus* and the separation of *Epistylum* from it, would correspond closely to the limits accepted in this treatment, and indicates that Jussieu had a good appreciation of natural affinities.

The next major revision of the Euphorbiaceae is that of Baillon (1858). Here fifteen genera of *Phyllanthus*-complex are accepted; *Emblia*, *Xylophylla*, *Gynoon* and *Anisonema* are reduced to synonymy, but *Williamia*, *Asterandra*, *Orbicularia*, *Zygosperrum*, *Melanthesa*, *Sauropus*, and *Glochidionopsis* are recognized. This treatment is the last one on a world-wide scale in which there is extensive fragmentation of the group originally circumscribed by Linnaeus as the genus *Phyllanthus*. In 1860 Baillon began the publication of a "Monographie des *Phyllanthus*," but shelved it after the writings of Mueller Argoviensis began to appear in 1863. In Baillon's unfinished monograph the genus has the same delimitation as in the 1858 work; but later Baillon adopted Mueller's very broad circumscription of the genus.

Contemporary with Baillon's work was that of Grisebach, of special interest since it deals with West Indian species. In the "Flora of the British West Indian Islands" (1859), he reduced *Epistylum*, *Anisonema*, and Baillon's *Orbicularia* to sections of *Phyllanthus*, but maintained *Cicca* as distinct. Grisebach, both in "Plantae Wrightianae" (1860) and in 1865, described several new species from Cuba and one additional new section, *Williamiandra*. Grisebach's work was not especially profound and he made some serious errors in distinguishing taxa and in suggesting relationships.

Overlapping the studies of Baillon and Grisebach are those of Jean Mueller of Argau (Mueller Argoviensis), who, between 1863 and 1866 published several papers on the Euphorbiaceae, culminating in the monographic treatment of the family in De Candolle's "Prodromus." This monograph begins a new era in the study of Phyllanthinae, for not only are all of the generic concepts proposed by various authors evaluated, but also the individual species are painstakingly and accurately described, with meticulous citation of synonymy and specimens. The few flaws in execution are far outweighed by the brilliant scholarship of the treatment, which is the more striking in being perhaps the most massive critical monograph of a plant family ever accomplished by a single individual.

At first, in his long paper in "Linnaea" (1863), Mueller accepted *Glochidion* as a genus distinct from *Phyllanthus*, distinguishing it on the basis of its unbranched styles, which equal in number the cells of the ovary. By 1865 he had changed his mind, and in the revision in the "Prodromus" *Glochidion*, along with many other segregate genera accepted by Baillon, was included in *Phyllanthus*. The genus *Phyllanthus* in the inclusive sense of Mueller was thus extremely heterogeneous, comprising no less than 44 sections. In the "Flora Brasiliensis" (1873) Mueller proposed a few new sections and species but made no important modifications.

Among the post-Linnaean work on the genus, that of Mueller stands preëminent and has exercised the strongest influence in the development of the generic concept. His monograph is still the basic reference source for any taxonomic study of the genus; and although various authors compiling regional floras have resurrected segregate genera or even proposed new ones, the generally prevailing concept of *Phyllanthus* owes its circumscription to Mueller.

Impressive as was Mueller's work, it did not go unchallenged by his contemporaries. Baillon (1873) sharply criticized Mueller's treatment for its lack of appreciation of general affinities. Many of Baillon's criticisms were certainly justified; nevertheless in his "Histoire des Plantes" (1874) he accepted precisely the same generic limits as those proposed by Mueller. Bentham (1878) contributed a very interesting paper, based on his research in preparation for the treatment of the Euphorbiaceae in the "Genera Plantarum," in which he evaluated the work of Baillon and of Mueller, and made some pertinent suggestions as to affinities. He accepted Mueller's delimitation of the genus, but grouped the sections into eleven "primary sections" which correspond roughly to the subgenera of the pres-

ent treatment. This arrangement was formally presented with synonymy in the "Genera Plantarum" (1880).

The only important modification of Mueller's generic concept was made by J. D. Hooker (1887), who restored *Glochidion* to the rank of a separate genus. His remarks are interesting enough to be quoted:

"I find it inexpedient to follow Mueller (in DC. Prodr. xv. ii. 278) and Bentham (Gen. Plant. iii. 272) in reducing *Glochidion* to a section of *Phyllanthus*, from which it differs in the total absence of a disk, in habit, and in the singular modification of its styles and stigmas. Further, by keeping it distinct I comply with the wishes of the Indian Botanists, whose opinion it is of importance to consult in regard to the nomenclature of so very large and universally distributed an Indian genus."

Pax (1890) adopted the generic limits as modified by Hooker, separating *Glochidion* from *Phyllanthus* but retaining both genera in the subtribe Phyllanthinae. In the second edition of the "Naturlichen Pflanzenfamilien" (1931) Pax and Hoffman transferred several sections of *Phyllanthus*, including *Hemiphyllanthus*, *Ciccastrum*, and the New Caledonian members of the *Gomphidium*-complex, to *Glochidion*. This was a step backward, for the 1890 arrangement appears to be closer to natural affinity. Croizat (1943) has rightly objected to the extension of the range of *Glochidion* to the New World, for the genus actually appears to be confined to Asia and Australasia. The various species from South America and Madagascar which have from time to time been placed in *Glochidion* seem best retained in *Phyllanthus*, even though they do belong to a primitive group that perhaps has some affinities with *Glochidion*.

Except for the work of Pax and Hoffman, there have been no comprehensive treatments of *Phyllanthus* in the twentieth century. There are, however, two "regional monographs" which merit special mention. C. B. Robinson (1909) published a revision of the Philippine Phyllanthinae which shows observation and originality. On the basis of its drupaceous fruit, he resurrected *Cicca* as a genus distinct from *Phyllanthus* (with which it had been combined by Mueller). Baillon (1858), although also maintaining *Cicca* as a distinct genus, had remarked that the fleshiness of the fruit is not a dependable character, since there is within *Phyllanthus* a nearly continuous gradation from dry capsules to drupes. In many species the fruit is quite fleshy until late in development, when it suddenly dries out and becomes capsular. This consideration probably influenced Mueller in his reduction of *Cicca* to *Phyllanthus* (1863). As Robinson's description indicates, however, the fruit of *Cicca* is actually more distinctive than other fleshy fruits of species of *Phyllanthus*:

"... fleshy externally, containing a 6- or 8-grooved bony endocarp, firmly united, and not separable by pressure, showing however by traces of the original carpellary walls on its exterior that it represents either 3 or 4 carpels, and containing 3 or 4 cells each with one seed."

A number of species of *Phyllanthus* have baccate or subbaccate fruits, and *P. emblica* has a drupe-like fruit resembling that of *Cicca*. But al-

though the endocarp of *P. emblica* is bony, it still separates into three cocci at maturity. The drupe of *Cicca* therefore is a good distinguishing character, as are the tetramerous flowers with the occasional production of staminodes in the females. Nevertheless, the pollen grains, seeds, and growth form are all quite typical for *Phyllanthus*. We have here a group which is on the borderline of generic status, and, despite all that has been written, one whose disposition — in our present state of knowledge — must be largely a matter of taste. *Cicca* is here retained as a subgenus of *Phyllanthus*, with the reservation however that additional study may perhaps justify Robinson's giving it generic status.

Leandri, in a considerable number of publications, has reviewed the *Phyllanthaceae* of Madagascar, where many interesting species occur. He upholds *Glochidion* and assigns several Madagascan species to the genus, but retains *Cicca* as a section of *Phyllanthus*. The species placed by him in *Glochidion* do, like those of sect. *Microgluchidion* in South America, have flowers and leaves quite suggestive of some New Caledonian species placed in *Glochidion* by Pax and Hoffman. But all these species, though forming a distinctive group and perhaps representing the ancestral form from which *Glochidion* was derived, appear best retained within *Phyllanthus*.

To conclude this survey, we have to review the concepts of those who have written on the West Indian species of *Phyllanthus* in particular. After Swartz, the first work of any importance was that of A. Richard (1850), who described some Cuban species. Grisebach, both in the "Flora of the West Indian Islands" (1859) and "Catalogus Florae Cubenses" (1866), recognized *Cicca* as distinct from *Phyllanthus*, but agreed with Mueller in relegating *Xylophylla* and several other groups to sectional rank. Wright (Flora Cubana, 1870) accepted the reduction of *Cicca* and described a few new species. Urban, in a long series of publications (1899–1930), described many species of *Phyllanthus* and often gave suggestions as to affinities. Although he published no keys or general discussions, his scattered comments are often quite to the point. Urban delimited *Phyllanthus* in the Muellerian sense, in marked contrast to N. L. Britton, who adopted a very radical conception of generic limits. The latter described from Cuba (1920) three new segregate genera — *Ramsdenia*, *Roigia*, and *Dimorphocladium* — and also recognized as genera *Conami* and *Orbicularia*. All of these, in the present treatment, are placed under *Phyllanthus*, and all except *Conami* in sect. *Orbicularia*. In Britton and Wilson's flora of Puerto Rico (1924) the species of *Phyllanthus* sensu Mueller are distributed among *Asterandra*, *Cicca*, *Conami*, *Margaritaria*, *Phyllanthus*, and *Xylophylla*; of these, only *Margaritaria* seems really generically distinct.

Recently Alain (1954) has presented a synopsis of the Cuban species of *Phyllanthus*, accepting the genus in the conservative delimitation and recognizing 65 species for the island.

When all treatments of the past seventy years are reviewed, it appears evident that the current generic concept of *Phyllanthus* is essentially that of Mueller amended by Hooker. As noted above, both Bentham and Baillon criticized Mueller's work on the basis that it did not take sufficient ac-

count of natural relationships. Bentham said of Mueller (and, with less justification, of Baillon) that he did not appear "to have sufficiently borne in mind the fact that characters differ in value in different genera or other groups. . ." Mueller, as Briquet (1896) pointed out, was an anti-evolutionist and had at first been interested in mathematics as much as in botany. Both these indications of his temperament are clearly reflected in his publications. His monograph in the "Prodromus," including keenly written descriptions of over 2,000 species in more than 1,000 species of text, is one of the triumphs of the descriptive method. But for the modern student it has a distinctly typological caste, i.e., "natural affinity" for Mueller does not appear to necessarily imply specific genetic kinship but is rather the expression of ideal relationships between mathematically definable entities. The Muellerian genus is, at least to some extent, a kind of Platonic idea of which the species are the earthly manifestations.

Nevertheless, in spite of their reservations as to Mueller's systematic criteria (and, by implication, his philosophic premises), Baillon, Bentham, and others accepted his system in the main. Although the general recognition of *Glochidion* as a genus partly altered the generic circumscription, the sections proposed by Mueller and his reductions of many groups to synonyms of *Phyllanthus* have gone largely unchallenged. This is in part due to Mueller's great authority, but also (and perhaps mostly) to the great size and unwieldiness of the genus. The present need is for a classification which will express phylogenetic relationships, and inevitably this will require drastic alterations of the Muellerian scheme. Pax and Hoffman, in the most recent (1931) general review of the genus, have — by merely adapting his system and driving the use of arbitrary characters to an even greater extreme — produced an uneven and, on the whole, unsatisfying classification.

The genera of Phyllanthaceae as recently maintained may aptly be compared to political boundaries which are superposed over the natural physiographic features of a region. "Phyllanthus" is the designation for all Phyllanthaceae in which the flowers are apetalous, lack a pistillode, and have a disk, or else do not fit into any other genus of Phyllanthaceae! "Glochidion" includes those plants in which the flowers are apetalous, lack both pistillode and disk, and have undivided styles. "Securinega," as Bentham pointed out, is an artificial genus in which are placed various plants related to *Phyllanthus* that have little more in common than a pistillode in the male flower.

It is apparent that not much more can be done toward constructing a new classification until a thorough morphological survey can be made of all the groups within the Phyllanthinae. Mueller, in his thoughtful critique of previous systems of the Euphorbiaceae (1866a), pointed out that one of the most glaring deficiencies of Baillon's monograph was that author's failure to study the groups beginning with the species level. It is because of this emphasis on the species as the fundamental entity that Mueller's studies are still so valuable today. Until the laborious job of analysis on this level is completed, taxonomic conclusions must necessarily be tentative,

and traditional circumscriptions of taxa accepted insofar as is possible. Nevertheless, studies already finished indicate that extensive changes, many of them nomenclatural, are immediately required, and more will be forthcoming for some time. However, it is hoped that this temporary instability in names will be compensated for by the increase in our knowledge of the biology of the organisms.

TECHNIQUES

During the course of this study, the examination of herbarium specimens and correlation of the literature have inevitably occupied a great deal of time. However, in order to advance beyond the concepts of previous workers it has been necessary to study the morphology of the plants in greater detail, using a few techniques in addition to those of standard herbarium practice. A rather sizable collection of herbarium sheets, pickled material, and seeds collected in Cuba and Jamaica has made fairly detailed investigations possible.

For analyzing the gross morphological features of herbarium specimens, a data sheet has been devised which also contains spaces to record observations on pollen morphology and leaf anatomy. Measurements of vegetative structure, fruits, and seeds were taken from dried specimens, but the flower parts (except for the calyces of female flowers) were measured in water. Refined statistical studies have not been attempted in most cases, but an effort has been made to take measurements from structures of comparable age and position. Thus, measurements of internode, stipule, and leaf blade dimensions are taken from the middle half of branchlets, unless specifically stated to the contrary. Organs abnormally developed or not fully mature have been avoided insofar as possible. However, it is not always easy to decide if a structure is fully or normally developed; unfortunately this is particularly true of the fruit and seed in *Phyllanthus*, for in some species the capsule is fleshy until late in development and in others it dehisces precociously on the drying of the specimen, whether mature or not.

The study of gross morphology presents a special problem in *Phyllanthus* because of the very small size of the flowers of many species. In many instances accurate observation requires magnifications of at least 30–50 diameters with substage lighting, and even then mistakes of observation are not precluded. In preparing dried flowers for examination, the most satisfactory method appears to be placing them in a solution of commercial photographic wetting agent; they may then be kept in small packets if reexamination is required. Commercial detergents such as "Dreft" accomplish the same end but are less satisfactory for the small-flowered species of *Phyllanthus* because they cloud the water and accumulate precipitates around the flower parts. Boiling is perfectly satisfactory for the larger flowers but is too destructive to the smallest delicate ones.

One of the chief annoyances encountered in the study of herbarium specimens was the recording of geographical data. The need for an historical

gazetteer of the West Indies becomes quite apparent to anyone who has tried to find old localities in Cuba or Hispaniola, for instance. However, Urban's bibliographic and historical notes in the "Symbolae Antillanae" (volumes 1 and 3) have helped a great deal to overcome this deficiency. For information on Cuban collectors, the summary by Leon (1918) and the discussion and map of Charles Wright's localities in Oriente Province by Jervis (1953) are especially useful. A detailed report on the explorations and collections of Ekman in Cuba and Hispaniola would certainly be appreciated by Caribbean botanists.

A better understanding of the relationships of many groups has been obtained by anatomical studies of the vegetative and reproductive structures, using the technique of cleared whole mounts as perfected by Wagner (1952) and by I. W. Bailey and his collaborators at Harvard. Individual leaves, portions of leaves, or entire flowers are first softened in potassium or sodium hydroxide for a few days; if preparations are needed quickly a few hours in heated potassium hydroxide are usually sufficient to treat even the most coriaceous leaf blades. The organs, which often are still quite opaque after this preliminary treatment, may then be bleached in 50% sodium hypochlorite until clear enough so that newsprint can be read through them. Then they are carefully rinsed in water, treated briefly in lactic acid, and stained overnight (or for a shorter period) in 50% alcoholic safranin. The tissues of most species of *Phyllanthus* appear to have a great affinity for safranin; successful preparations have been made from material left in the dye without heating for as little as thirty minutes. Following the standard method of Johansen (1940) the material is differentially destained in 95% alcohol saturated with picric acid, followed by brief immersion in 95% alcohol to which a few drops of ammonia have been added. If the material is thin, it can then be removed directly from 95% alcohol and mounted in diaphane. Very thick coriaceous leaves, however, are best transferred to absolute alcohol for a few minutes in order to reduce the chances of contamination by water. Fast green was tried as a counter-stain but proved unsatisfactory because it acted so rapidly that uniform differentiation within thick mounts was impossible. Safranin alone is perfectly satisfactory; in good preparations one can study stomata, epidermal cells, and mesophyll almost as well as the vascular strands. Foster's tannic acid method (1934) did not prove very successful with whole mounts of leaves of *Phyllanthus* because differential staining was too uneven.

No special difficulties were encountered in making microtome sections of flowers and stems and staining them with safranin and haematoxylin or fast green. Macerations of the wood of several species were also prepared to show vessel structure; these were mounted in diaphane. Free-hand sections of twigs of several species were stained with aniline blue, and slides of the species available in the Harvard wood collection were studied.

Some of the most interesting morphological data were obtained from whole mounts of pollen grains, following the technique suggested by Wodehouse (1933). The grains were squeezed on a slide by manipulation of a wetted flower and washed with 95% alcohol to remove the oil globules

adhering to them. A bit of methyl-green glycerine jelly on the tip of a dissecting needle was then touched to the grains until several of them adhered. Another clean slide was heated on a warming plate and the bit of glycerine jelly melted on it. Following the suggestion of Erdtman (1952), many mounts were prepared by placing a no. 1 circular coverslip over the jelly and running melted paraffin under the edge of the coverslip; the paraffin cools quickly and forms an air-tight seal. Continued experience, however, has shown that this method has some serious disadvantages. The paraffin seal is not durable and consequently the slides must be carefully protected and handled with great care. Furthermore, the refractive index of the glycerine jelly is not satisfactory for accurate inspection of many pollen grains. Recently, mounts have been prepared by placing the grains in lactic acid and sealing the rim of the coverslip with ordinary transparent nail-polish; exine details appear to be much clearer with slides of this type, but how long they will last remains to be seen.

Occasionally other techniques have been used to a minor extent for specific structures. Often the leaves and flowers of some species of *Phyllanthus* remain somewhat opaque even after treatment with potassium hydroxide and sodium hypochlorite. These are best studied after immersion in chloral hydrate solution for one or several days; this is particularly useful for fruits and seed coats. Microchemical tests on seed coats and leaves to determine the presence of lignin, suberin, and cellulose yielded some interesting results, and offer considerable promise for further investigations. Cytological techniques present many difficulties because of the small size of flowers and of the individual chromosomes as well as of the large numbers of chromosomes in the woody forms, but the results should be interesting enough to warrant some effort.

GROWTH FORM

As a preliminary to a detailed consideration of the morphology of vegetative and reproductive organs, the following survey of the different types of branching in *Phyllanthus* is presented.

Many of the current systematic difficulties in the Phyllanthinae are directly traceable to the lack of appreciation of vegetative structure displayed by Mueller Argoviensis. Mueller was aware of some of the differences in habit, but since he took the Linnaean view that only floral differences were of importance in defining supraspecific taxa, he only utilized the branching type to separate a few species in sections *Phyllanthus* and *Paraphyllanthus*. Nowhere did Mueller demonstrate a thorough appreciation of the significance of growth form within the genus, despite his accurate observations on minute details of floral morphology. The reason evidently lies in his lack of acquaintance with the living plants; the different types of growth form are often far from obvious with fragmentary specimens.

Hermann Dingler (1885), in his important though almost completely neglected work on the phylloclades of *Phyllanthus* sect. *Xylophylla*, was

the first (and only) author to present a comprehensive and accurate analysis of the different modifications of growth form in the genus. He not only demonstrated convincingly the derivation of the plants with phyllclades from less specialized types, but also discussed the evolution of growth form throughout the entire genus. Unfortunately, the striking results of Dingler's study were largely passed over by morphologists and systematists. In the last general review of the genus, Pax and Hoffman (1931: 61) were content to observe that the "*Niruri*-Typus" occurred in different sections; they still retained within the Muellerian sect. *Euphyllanthus* some of the vegetatively most diverse species of the genus. In the following discussion the species of *Phyllanthus* will be considered under four classes, based on the branching pattern.

Type I. As Dingler recognized, a comparatively small number of species of *Phyllanthus* have what may be termed a completely unspecialized kind of branching. *Phyllanthus polygonoides*, a widespread species of Mexico and the southwestern U.S., and its close relative, *P. platylepis* of Florida, may serve as examples of this group (PLATE-FIG. 1). Here the phyllotaxy is completely spiral and the axes are all equivalent. The only noticeable specialization is the varying length of stems and their internodes. In *P. polygonoides*, for instance, a leafy "winter rosette" analogous to that in *Panicum* subg. *Dichantherium* is formed by shortened branches from the lowermost axils.

Many of the species in this class are vegetatively quite similar to species of *Andrachne*, but have very different apetalous flowers without pistillodes, so that the resemblance is presumably due to parallel evolution. In addition to the North American *P. polygonoides* and its relatives, several Australian species such as *P. calycinus* and *P. thymoides* have completely spiral phyllotaxy.

A number of species, both herbaceous and woody, have stems with the phyllotaxy spiralled below and distichous above. Herbaceous examples are some of the species related to the widespread Old World species *P. maderaspatensis*; the differentiation here is very slight, for the same axis may have leaves spirally arranged below and distichous above, and the inflorescences may be borne indiscriminately on any axis. These species form a transition between types I and II without, however, reducing the value of distinguishing between the classes.

Type II. In *P. caroliniensis* of sect. *Loxopodium* and *P. virgatus* of sect. *Macraea* the phyllotaxy is, at least after the first few nodes above the cotyledons, completely distichous. However, since flowers may occur at any node, there is still no differentiation of axes. Most of the representatives of this class, which includes the only really temperate species, are herbaceous, but some of the tropical species are definitely shrubs. Correlated with the distichous phyllotaxy is a trend toward more or less flattened stems with two lateral angles or wings; this line of development culminates in the Tahitian *P. aoraensis*, which has broadly winged stems similar to those in some of the tropical Loranthaceae.

Type III. A number of woody species, such as *P. grandifolius*, *P.*

nutans, and *P. pachystylus* (PLATE-FIG. 2) of sect. *Elutanthos*, present a somewhat different kind of predominantly distichous phyllotaxy. Here the seedling axis appears to bear spiral leaves, but the lateral axes all have distichous leaves except occasionally at the first few nodes on a lateral branch. In a mature, copiously branching plant of this type, the branches coming off the main stem are all alike, bearing flowers (at least potentially) at every node and producing similar branches more or less indiscriminately from the same or different nodes as the flowers.

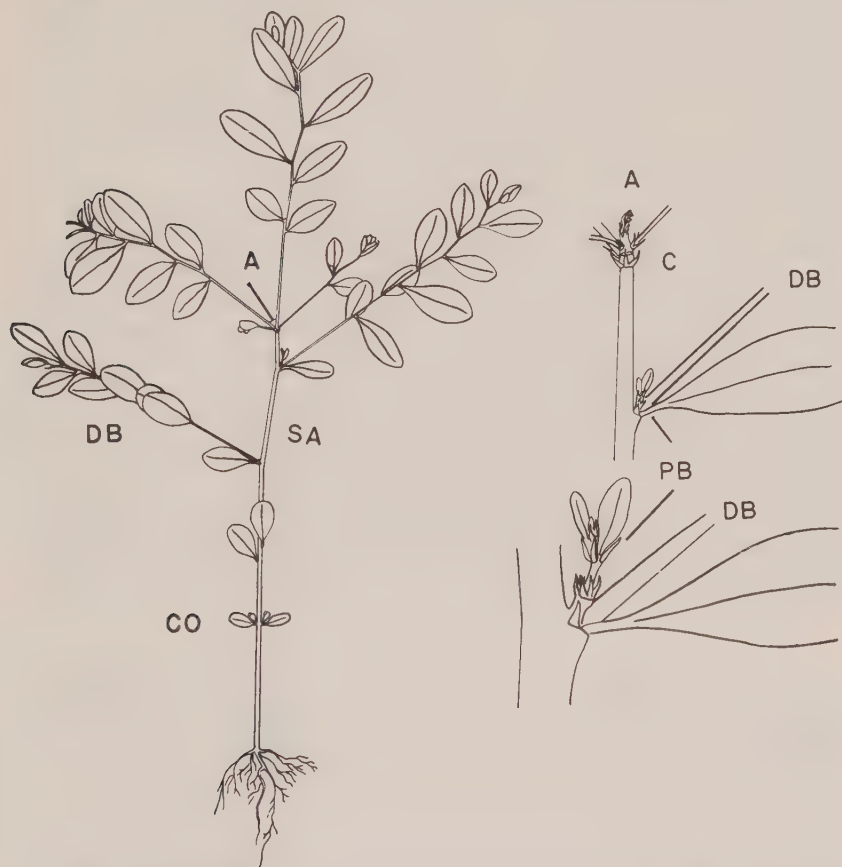
Not only is this sort of growth-form probably the most common one among tropical alternate-leaved shrubs of all families, but the same pattern of distichous-leaved lateral shoots borne by a primary axis with spiral phyllotaxy is exhibited by the seedlings of many of our familiar temperate trees such as *Celtis*, *Quercus*, *Fagus*, and *Tilia*. A common characteristic of all these plants is the persistence and essential similarity of the axes which produce flowers and new branches.

Type IV. The great majority of both the woody and herbaceous species of *Phyllanthus*, however, have a growth form radically different from those just described. In the plants of this type there are two completely different kinds of axes; the penultimate axes have spiral phyllotaxy with leaves modified as cataphylls which subtend deciduous, floriferous, distichous-leaved ultimate axes. The stems, in other words, are differentiated into persistent, flowerless, "leafless" long-shoots, and deciduous, floriferous, "leafy" short-shoots. Since this specialized type of growth form characterizes over 550 of the 650 species in the genus, it seems appropriate to designate it as *phyllanthoid branching*.

It is not surprising that among so many species there should be some unusual modifications of phyllanthoid branching. We may first profitably examine the typical situation in a species which may be clearly related to the less specialized types in the genus. As an example, a common annual weedy species, *P. tenellus* (TEXT-FIG. 1; PLATE-FIG. 3) may be useful. The seedling of *P. tenellus* usually bears normal leaves with expanded blades at the first four nodes above the cotyledons; then, however, there is an abrupt change, for the subsequent leaves on the main axis are all scale-like cataphylls. The first two lateral axes, at nodes 3 and 4, are subtended by normal leaves, but the rest are all subtended by cataphylls.

These lateral short-shoots have a very characteristic form. The proximal internode (in *P. tenellus*) is very long and the succeeding ones much shorter, so that the gross appearance of the branchlet is that of a petiole pinnately compound leaf, and it was indeed regarded as such by the botanists of the Linnaean era. It further resembles a leaf in its limited growth and regular abscission; and in *P. amarus* and many other herbaceous species the leaves fold together along the branch-axis at night in the manner of the leaflets of a leguminous leaf. *Phyllanthus urinaria* is reported to imitate *Mimosa pudica* by responding to touch with a slow folding up of the leaves. A number of species agree with *P. tenellus* in having a distinct pulvinus at the base of the pseudo-petiole. The superficial resemblance to leguminous leaves may thus become very close indeed, but these lateral

axes of *Phyllanthus* differ, of course, in the production of flowers in the axils of most or all of the leaves. This specialized kind of short-shoot will be referred to in this work as the *deciduous branchlet*.

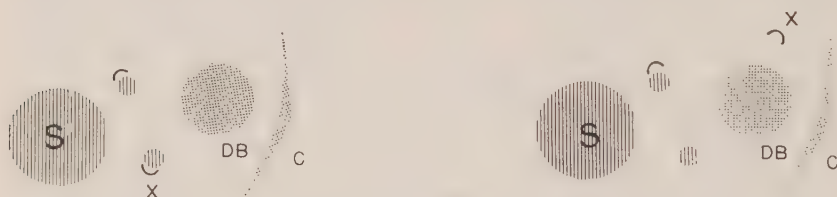


TEXT-FIG. 1. Seedling of *P. tenellus* Roxb., showing phyllanthoid branching. A, stem apex; C, cataphyll; CO, cotyledon; DB, deciduous branchlet; PB, permanent branch; SA, seedling axis. The apical region is shown in enlarged view on the right.

As its name implies, the deciduous branchlet does not carry on the branching of the plant; but in its axil occurs a bud which may expand into a long-shoot that morphologically resembles the seedling axis, i.e., it bears spirally arranged cataphylls each of which subtends a deciduous branchlet. The long-shoot, which bears only floriferous branchlets (never flower-clusters) in the axils of the scale-leaves, has often been referred to as the "penultimate branch" in systematic literature. However, it seems more feasible to designate it as the *permanent branch*. For the sake of brevity, the two types of stems may be referred to as "branch" and "branchlet."

Phyllanthoid branching is thus the distinctive pattern resulting from the orderly concatenation of deciduous and persistent axes. Typically, a deciduous branchlet and the bud of a permanent branch (which may or may not develop) are produced at each node on the main axis. In herbaceous species such as *P. tenellus* the branchlet and branch may appear collateral, but in woody species such as *P. discolor* the branch definitely appears to be in the axil of the branchlet. Actually, close inspection shows that even in the herbaceous species the branch arises axillary to the branchlet, although its position later shifts. The unexpanded permanent branch is therefore an accessory bud in the classical definition (cf. Gray, 1879: 44). However, Dingler (1885: 23–25), on the basis of his studies of ramification in *Phyllanthus*, advanced the theory that the permanent branch bud ("Beiknospe") is not an independent or "accessory" structure but rather represents a branch from the first node of the deciduous branchlet. He assumed that the first internode of the branchlet is so greatly shortened that the two axes appear to originate at the same level.

The spatial relationships of bracts and axes appear to support this concept. The scale which subtends the permanent branch lies obliquely opposite the cataphyll subtending the branchlet and adjacent to the main axis (TEXT-FIG. 2a). If the reverse assumption — that the branchlet is produced from the base (first node) of the branch — is made, then the latter should lie adjacent to the cataphyll subtending the branchlet rather than adjacent to the main axis (TEXT-FIG. 2b). The fact that this has never



TEXT-FIG. 2. Diagrams indicating the alternative possible positions of scales and axes at the node of a species with phyllanthoid branching. The cataphyll (C, here shown undivided for the sake of simplicity) and deciduous branchlet (DB) are shown stippled; the main stem or branch (S) and the two small axillary permanent branch buds (unlabelled) are shown lined. In the diagram on the left (2a) the scale or cataphyll (X) subtending the first permanent branch lies between the branch and main stem; this is the situation observed in living plants. In the hypothetical alternative shown in the diagram on the right (2b) the scale (X) lies on the other side of the deciduous branchlet.

been observed suggests that Dingler's idea is probably correct, so that the permanent branch may be regarded as derived from a lateral branch of the deciduous branchlet.

A further complication, however, arises with the development of the primordium of another permanent branch in the axil of the first one. Normally this second permanent branch remains arrested as a small bud but

occasionally it expands; there may even be four or five permanent branches produced at a node, each axillary to and theoretically springing from the base (lowermost node) of the one preceding. A perhaps more satisfying conception of this might be to regard the deciduous branchlet and its axillary permanent branches as a whole shoot, the lowermost branch of which has become a specialized dorsiventral structure divergent from the remaining radial branches. This would take care of a difficulty raised by the pattern of seedling development in several species. In *P. amarus* and *P. tenellus*, for example, permanent branches may occur at the cotyledonary and successive two nodes, where there are never any deciduous branchlets developed. If permanent branches are considered as ramifications of deciduous branchlets, it might be wondered how they could arise at these nodes where their "mother-axes" are missing. But on the basis of the "whole-shoot" concept, the interpretation would be that the suppression of the deciduous branchlets at the lowermost nodes, which is correlated with expanded leaf-blades, does not affect the permanent branches. It may be recalled here that the "competition" between the foliage leaf of the main axis and the leaf-like branchlet usually results in an inverse correlation of their relative development.

The systematic implications of phyllanthoid branching are nicely shown in considering the relationship between *P. tenellus* and *P. amarus*. The latter has a very similar seedling development, differing chiefly in the minor points that the first deciduous branchlet (from node 3) is sterile and that the permanent branches develop from nodes 1 and 2 much less precociously than in *P. tenellus*. Mueller placed these two species in the widely separated sections *Menarda* and *Euphyllanthus* on the basis of stamen number; but the similar growth form and pollen grains suggest that the two species are more closely related than previous taxonomic systems would suggest. Many similar instances of unnatural classification due to lack of recognition of growth forms could be adduced. On the other hand, it must be remembered that phyllanthoid branching *per se* is not necessarily an accurate guide to affinity. *Phyllanthus urinaria*, for example, has a growth form very similar to that of *P. amarus*, but it appears to be more closely related to the species of sect. *Loxopodium*, which have distichous branching. Apparently phyllanthoid branching has arisen more than once in unrelated sections of the genus, so that its taxonomic significance, though often great, must be interpreted with care.

The seedlings of *P. tenellus* and *P. amarus* have been described as having a single long-shoot, the main seedling axis, which bears the deciduous branchlets. But in older plants of these species, or ones which have been injured in some way, several of the "accessory buds" may grow out into long-shoots and the plants may thus become considerably branched. In related perennial species such as *P. abnormis* the dominance of the apical meristem is short-lived, the adult plant then developing several main branches. Among many of the herbaceous perennial species, particularly of sect. *Phyllanthus*, there is a phylogenetic trend toward loss of dominance of the apical meristem. This reaches an extreme stage in *P. pentaphyllus*,

where the primary axis becomes abortive just above the cotyledons and a cluster of wiry permanent branches grow out as coordinate main stems. The resulting habit is analogous to that in some species of *Euphorbia* subg. *Chamaesyce*, as illustrated by Croizat (1937).

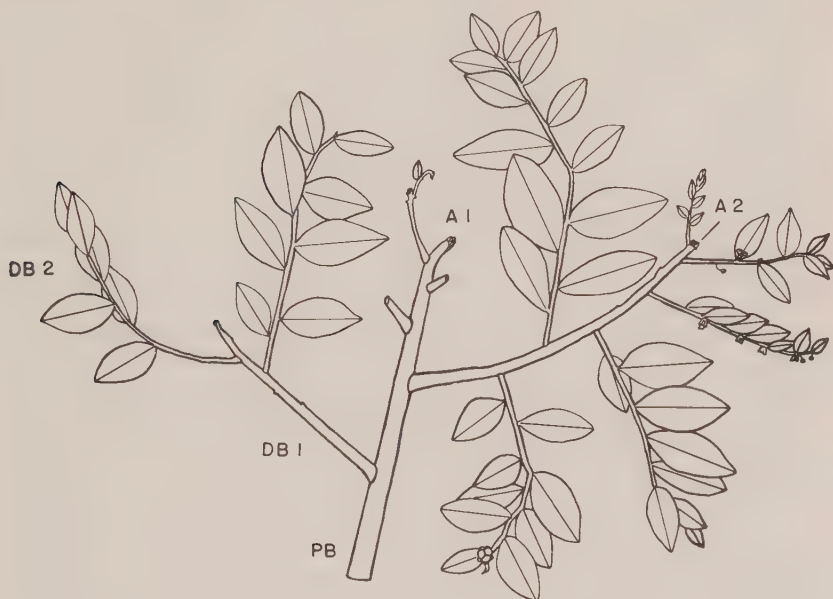
Many of the shrubby species of *Phyllanthus* probably have a growth sequence basically similar to that in *P. tenellus*, although in most cases their germination and early seedling development has not been followed. In some species such as *P. juglandifolius* of sect. *Asterandra* the permanent branches may be almost or entirely suppressed; the plants then have a palm-like or tree-fern-like ("schopfbaumartig") habit, with leafy branchlets clustered at the apex of an unbranched trunk (PLATE-FIG. 4). In other woody species, such as *P. orbicularis*, the permanent branches become well-developed and the mature plants consequently have a bushy habit.

Another complication of phyllanthoid branching is displayed by those species in which "secondary short-shoots" occur. A number of West Indian species show this phenomenon to some extent, *P. subcarnosus* being one of the best examples. Here there is superimposed on the basic pattern of permanent branch and deciduous branchlet a differential elongation of the internodes of the permanent branches. The result is that most of the current leafy branchlets will be found clustered at the tips of spur-shoots. This sort of development, which is comparable to the short-shoot development in *Ginkgo*, should not be confused with phyllanthoid branching, for there is no important morphological difference between long-shoot and spur-shoot.

In some species with this kind of development the spur-shoots may become so reduced that several deciduous branchlets will appear to be fascicled at the same node; the commonly cultivated *P. emblica* provides the most familiar example. In *Phyllanthus*, the cauliflorous condition appears to have arisen by a combination of extreme spur-shoot development and the differentiation of the deciduous branchlets into "leafy" sterile and "leafless" fertile axes. The result is the production of sterile leafy branches at the ends of twigs, with the flowering branchlets (the leaves often reduced to scales) developing further back at nodes from which the leafy branchlets of the previous year have fallen. *Phyllanthus emblica* has travelled part of the way toward cauliflory, for it does have fertile and sterile branchlets; but the fertile branchlets still have the leaves reduced only at the proximal end. In *P. acidus* and *P. cauliflorus* true cauliflory is achieved, but both species also produce some partially leafy fertile branchlets. In *Phyllanthus* the cauliflorous condition never reaches such an extreme state that there is no flower production by normal leafy branchlets.

So far phyllanthoid branching has been discussed with regard to those species having what may be termed "pinnatifid" branchlets, i.e., branchlets with an unramified main axis on which the leaves are attached in the manner of leaflets on the rachis of a simply pinnate leaf. But there are at least 25 or 30 species, belonging to three different sections, in which the branchlets are "bipinnatifid." In *P. ovatus* of the West Indian section *Hemiphyllanthus*, for example, the branchlet consists of a main rachis with

the leaves reduced to cataphylls but in distichous arrangement (TEXT-FIG. 3). Each cataphyll subtends a leafy floriferous lateral axis which is comparable to the entire pinnatifid branchlet of *P. amarus* or *P. juglandifolius*, but (as shown below) not homologous with it.



TEXT-FIG. 3. Branch of *P. ovatus* Poir., a species with bipinnatifid deciduous branchlets. A 1, apex of branch; A 2, apex of primary axis of branchlet; DB 1, primary (penultimate) axis of branchlet; DB 2, secondary (ultimate) axis of branchlet; PB, permanent branch. The cataphylls subtending the ultimate axes have been omitted from the drawing.

The bipinnatifid branchlets of the species of sect. *Nothoclema* are less specialized, for normal foliage leaves are borne at all the nodes of both primary and secondary axes. In such species as *P. subglomeratus* flowers also occur at all the nodes of both axes, while in others such as *P. acuminatus* flowers may be nearly or completely confined to the lateral axes. *Phyllanthus acuminatus* has an especially interesting branching pattern: each new permanent branch (arising from the axil of a branchlet of the previous year) produces about 3-6 branchlets, the first one pinnatifid but the succeeding ones all bipinnatifid. This not only shows that pinnatifid branchlets may be derived from bipinnatifid ones by reduction, but also demonstrates that the pinnatifid branchlet is homologous to the entire bipinnatifid one rather than to one of its lateral axes.

It by no means follows, however, that pinnatifid branchlets all represent reduced bipinnatifid ones. As a matter of fact, the species with

bipinnatifid branchlets belong to rather advanced sections of the genus; and the branchlets of the species that appear to have the most primitive kind of phyllanthoid branching are all pinnatifid. These species with ramification that appears transitional between phyllanthoid and unspecialized branching are, of course, especially interesting. In *P. sellowianus* of South America and *P. gunnii* of Australia, deciduous floriferous branchlets are produced but the leaves on the main axes (permanent branches) are usually not reduced to cataphylls. This condition, which is probably primitive in these two woody species, may be simulated in specialized herbaceous species such as *P. niruri* or *P. berterianus*, which may sometimes produce foliage leaves at all but the very highest nodes on the main axes. In this instance, however, the occurrence of unreduced leaves seems clearly correlated with the suppression of deciduous branchlets.

In all four species mentioned above the branchlets are deciduous with distichous phyllotaxy, and are the only axes bearing flowers. These are the decisive characteristics in the definition of phyllanthoid branching. The deciduous character of the branchlets should be emphasized, for the leaf-mimicking quality contingent on this feature is what gives such a distinctive aspect to the species with phyllanthoid branching. There doubtless is a correlation between the restriction of flowers to the lateral axes and their deciduous character. The evolution of phyllanthoid branching may therefore be crudely visualized to have taken place in two steps: first, the change from numerous equivalent axes with spiral phyllotaxy to a single erect main spiral-leaved stem with dorsiventral lateral branches; and second, the restriction of inflorescences to the lateral axes together with a loss of the capacity of the axes for unlimited growth. Dingler (1885: 87) visualized the predominance of the main axis over the laterals, which is a necessary prerequisite to the origin of phyllanthoid branching, as a result of the adaptation of the plant to competition with other individuals. This idea is supported by ecological studies of the tropical rain-forest which have shown that there is indeed among seedlings an intense competition for the available light and a resulting selective premium on speeded-up ontogeny. Consequently phyllanthoid branching may be imagined as an adaptation largely established by the effects of seedling competition of plants of a specific constitution. The entire, relatively small, not excessively sclerified leaves of the vegetatively unspecialized species of *Phyllanthus* may thus be conceived as "pre-adapted" for the evolution of leaf-like deciduous branchlets.

Dingler (1885: 97) noticed that the vegetatively unspecialized species of *Phyllanthus* (those with spiral phyllotaxy) show a significant ecological correlation, viz., they occur in open habitats in dry regions where there is not an intense competition for light, either between individuals or between stems on the same plant. This is doubtless true, but it would be incorrect to conclude thereby that these species are necessarily the most primitive type in the genus. There is no evidence that any species with unspecialized branching has evolved by reversion from a species with phyllanthoid branching. But slightly specialized forms such as the distichous-leaved

species of sect. *Elutanthos*, which seem to have no strictly determined vegetative structure, might well have given rise to species with spiral phyllotaxy and thus seemingly more primitive growth form.

The pervasive specialization of growth form in *Phyllanthus* culminates in the species of sect. *Xylophylla*, in which the branchlets have become leafless phylloclades. Dingler, who was the first to make a thorough investigation of the phylloclade-bearing species, suggested that the South American species of *Xylophylla* sensu Mueller were derived from "zweiaxigen" ancestors (i.e., species with pinnatifid branchlets), while the West Indian species were derived from "dreiaxigen" progenitors with bipinnatifid branchlets. This suggestion of the independent origin of phylloclades within the genus, though seeming perhaps improbable at first glance, has been decisively confirmed in the present study. Unfortunately Dingler obscured his point by claiming (1885: 101, 135-136) that the five species-groups which he recognized in *Xylophylla* represented parallel lines, each originating independently from different "beblätterten" ancestors. However, it seems most probable that the phylloclade-bearing species of *Phyllanthus* originated from only two ancestral groups. The South American species, which have probably been derived from representatives of sect. *Phyllanthus* with pinnatifid branchlets, must be grouped together in sect. *Choretropsis*. Section *Xylophylla* must be restricted to the West Indian species, which have probably been derived from sect. *Hemiphyllanthus*, the members of which have bipinnatifid branchlets.

Dingler (1885: 94-95) further made the interesting conjecture that the origin of phylloclades in the West Indian species did not represent a xerophytic adaptation as it probably did in the South American ones. He suggested instead that in the *Xylophylla* group a slight alteration in environmental conditions was probably sufficient to favor increased development of the lateral axes at the expense of the leaf-blades.

The homologies of the different types of phylloclades were investigated by Dingler (1885: 18-19), who demonstrated that the simple phylloclade of *P. epiphyllanthus* (TEXT-FIG. 4) has been derived by reduction from the compound one of some species such as *P. latifolius* or *P. speciosus* (= *P. arbuscula*) (TEXT-FIG. 5). Part of his supporting evidence was the observation that *P. epiphyllanthus* occasionally produces compound phylloclades while *P. arbuscula* occasionally produces simple ones. His report that *P. arbuscula* bears simple phylloclades on the seedling axis which are succeeded above by compound ones has been confirmed by personal observation, in Jamaica, of seedlings of this and other related species. The suggestion that the simple phylloclade represents a "Hemmungsbildung" of the compound one is supported by this evidence and by the observed reaction of a plant of *P. × elongatus* to pruning. The latter normally bears compound phylloclades, but when a main branch is pruned off the first phylloclades arising on the branches from the axillary buds are simple and very similar to those of *P. epiphyllanthus*. The origin of simple phylloclades is therefore analogous to the production of reduced leaves (cataphylls) on the lower part of the shoot of many plants, or to the occurrence of the

initial pinnatifid branchlet, followed by bipinnatifid ones, on the new shoot of *P. acuminatus*.

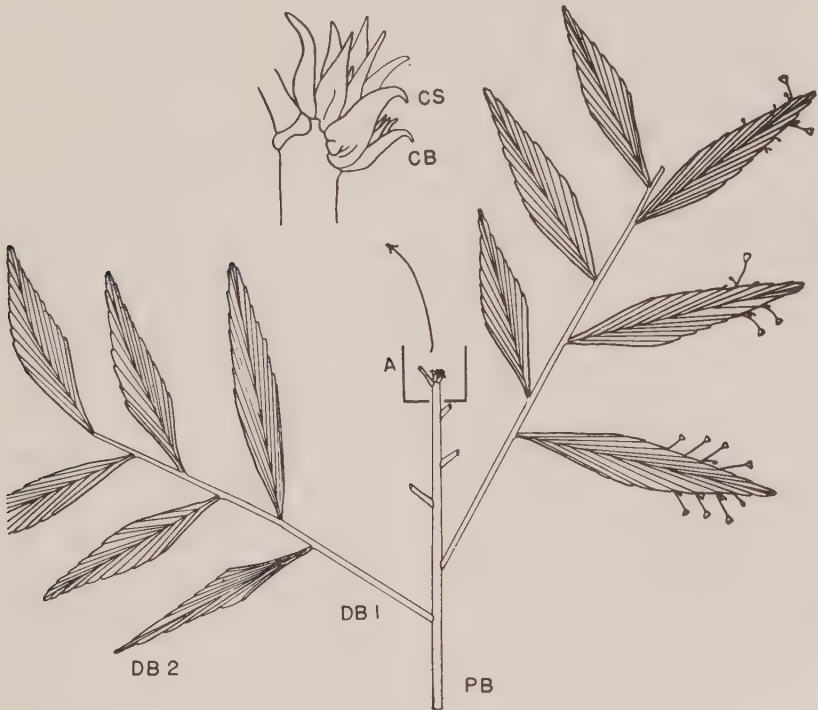
The systematic importance of phyllanthoid branching remains to be considered in its more general implications. Most, and probably all, of the species of *Breynia*, *Glochidion*, and *Sauropus* appear to have typical phyllanthoid branching; this, and evidence from floral morphology, strongly suggests that these genera are derived from *Phyllanthus* or from a closely related ancestral form. The subtribe Phyllanthinae could therefore be



TEXT-FIG. 4. Branch of *P. epiphyllanthus* L., a species with simple phylloclades. A, scaly apex (the meristem covered by aggregated cataphylls); C, cataphyll (the blade and stipules fused into a single structure in this species); DB, phylloclade; PB, branch or main stem.

characterized by phyllanthoid branching, except for the fact that a considerable number of species of *Phyllanthus* have less specialized growth forms. It is true that *Phyllanthus* as construed by Mueller and by Pax and Hoffman is polyphyletic, but even when obviously discordant groups such as *Margaritaria* are removed, there still remain over fifty species of *Phyllanthus* which have more or less unspecialized branching patterns. As will be shown later in the present study, the simple procedure of putting the species with phyllanthoid and non-phyllanthoid branching into two different genera will not work, because it obviously violates natural affinity. Not only are there close relationships between species with and without phyllanthoid branching, but it appears likely that this specialization has arisen more than once within the genus. Consequently, phyllanthoid branching, despite its importance, cannot unqualifiedly be used to define the subtribe Phyllanthinae or its constituent genera.

It is not yet clear how widespread phyllanthoid branching is among other groups of angiosperms. It has already been remarked that genera



TEXT-FIG. 5. Branch of *P. arbuscula* (Sw.) Gmel., a species with compound phylloclades. A, scaly apex, shown considerably enlarged above; CB, cataphyll blade; CS, stipule of cataphyll; DB 1, primary (penultimate) axis of phylloclade; DB 2, secondary (ultimate) axis of phylloclade; PB, branch or main stem.

such as *Celtis*, *Quercus*, *Fagus*, and *Tilia* represent a relatively unspecialized condition. The seedling of any one of these genera has a main axis bearing spirally arranged foliage leaves which subtend more or less dorsiventral lateral shoots. The leaves on the main axis are not modified into cataphylls and the ultimate branches are not ordinarily deciduous, so that these plants represent a stage equivalent to that of *P. nutans* (sect. *Elutanthos*).

There are a few temperate genera which show a closer approach to phyllanthoid branching. In both *Pinus* and *Berberis* there are long-shoots bearing spiral cataphylls which subtend short-shoots of limited growth. In *Berberis vulgaris*, as illustrated by Gray (1879: fig. 234), the long-shoot has at the base one or more nearly typical leaves, but the succeeding ones become more and more spine-like until the upper nodes bear only three-pronged spines. The chief differences from phyllanthoid branching are the gradual transition from foliage leaf to cataphyll and the presence of radial non-deciduous shoots. The leafy short-shoots of *Pinus* are much more limited in growth than those of *Berberis* but still are radial, and furthermore do not bear reproductive structures. Thus although *Pinus* and *Berberis* show a certain approach to the growth form prevalent in the Phyllanthinae, their branching patterns are not specialized enough to be classified as phyllanthoid.

So far the only plant outside of the Phyllanthinae in which phyllanthoid branching has been observed is *Casearia sylvestris* (Flacourtiaceae), living plants of which were examined in the Atkins Gardens, Soledad, Cuba. In this species the leaves on the main axis are reduced to cataphylls and the lateral axes are floriferous, leafy, deciduous branchlets; the resulting habit of the plant is quite similar to that of such species of *Phyllanthus* as *P. juglandifolius*. *Casearia*, like *Phyllanthus*, shows considerable diversity in growth form, for many species in the genus certainly have non-phyllanthoid branching. It is not impossible, of course, that phyllanthoid branching may be found in other genera of the Flacourtiaceae or in other families with tropical woody representatives. The various genera with the habit of miniature trees ("Schopfbaumchen") would be apt to exhibit approaches to or modifications of phyllanthoid branching. There are a number of interesting evolutionary problems connected with this possibility. Richards (1952: 76-77), for instance, has observed that the majority of the shrubs in the tropical rain forest have the Schopfbaum habit and has suggested that these plants should be regarded as procociously reproducing trees. This does not appear to be the case in *Phyllanthus*, but it would be interesting to investigate the problem in other families.

STEM

The morphology of both the vegetative and floral parts of *Phyllanthus* may be profitably discussed in close conjunction with their anatomy. This is particularly apropos in the Euphorbiaceae, where anatomical studies have played a systematically significant role. The family was one of the

first to be thoroughly investigated from the standpoint of correlating anatomy with systematics; Pax (1884) initiated this phase of study in the Euphorbiaceae by applying anatomical criteria to test the validity of the various suprageneric groupings proposed by Mueller, Baillon, and Bentham. Since Pax became the chief authority on the systematics of the family, an emphasis on anatomical definition of the taxa tended to be maintained.

Subsequent to Pax's classical paper, the Munich school of anatomists led by Radlkofer greatly extended the knowledge of the anatomy of the Euphorbiaceae by investigating several tribes in greater detail. The researches of most direct interest here are those of Froembling (1896), who worked with the Muellerian subtribe Euphyllanthaeae. He studied 87 species of *Phyllanthus* sensu Mueller; but in interpreting his results it must be remembered that about 20 of these have subsequently been removed to other genera (mostly to *Glochidion*). Rothdauscher (1896) provided a good report on the Phyllanthaeae other than the Euphyllanthaeae which summarizes data of value for anatomical comparisons of *Phyllanthus* with related genera.

Comparatively little detailed histological work has been done on the Phyllanthaeae in subsequent years. Gaucher (1902) presented an anatomical survey of the Euphorbiaceae which contains some information of interest. Unfortunately, however, he either ignored or was unaware of the work of the Radlkofer school, and as Solereder (1908: 1048) has pointed out, some of his reports are at variance with those of previous workers. He considered only 20 species of *Phyllanthus* and did not discuss most of them individually. Dehay (1935) has contributed an interesting monograph on the vasculature of leaf and petiole in the Euphorbiaceae which deserves to be followed up by further research. There seems little doubt that the technique of petiolar cross-sections offers considerable promise in defining some of the intrafamilial groups.

Most recently Metcalfe and Chalk, in their "Anatomy of the Dicotyledons" (1950, based on the compendium of Solereder, 1899), have summarized the anatomical information on the family. Their digest of the many papers is valuable, although their bibliography shows some notable gaps in the systematic anatomy of the Euphorbiaceae.

Despite the relatively large amount of anatomical work which has been done on the family, however, it is apparent that a comprehensive synthesis of this information with evidence from other fields such as gross morphology and cytology has not been attempted. An assimilation of what has already been accomplished is required in order to pinpoint the outstanding problems. The intensive investigation of these would then go far toward improving the classification of this large and difficult family.

The aim of the present treatment is to bring together what has specifically been published on *Phyllanthus* and to add personal observations on preparations of West Indian material. These studies have not so far shown anatomical characters to be of any great use in distinguishing closely related species, but as Pax suggested, they are of particular value in indicating affinities between groups of supraspecific rank. Here anatomical

distinctions may sometimes prove invaluable in suggesting whether certain floral characters represent true affinity or only parallel evolution. In some of the following discussions, therefore, the features observed in *Phyllanthus* will be compared with those in other genera and tribes. The root will not be given any special attention, since it does not appear to show any interesting modifications. Since the gross morphology of the stem has been discussed in the preceding section on growth form, the present consideration of the stem will center on internal characters as seen in macerations and in sections of twigs and mature wood.

Pax (1884: 413), in establishing the tribes and subfamilies of Euphorbiaceae on an anatomical basis, distinguished the Phyllanthoideae from the Crotonoideae on the basis of its lack of both intraxylary phloem and laticifers. He could distinguish the Phyllanthae from the Brideliaceae, however, only on the basis of the production of secondary bast fibers in the latter and their absence in the former. Subsequent observations have in the main confirmed these diagnostic characters but have so far contributed little to the definition of the subtribes.

As a typical example of young stem structure in *Phyllanthus*, the widespread tropical shrub, *P. reticulatus* var. *glaber* may serve (PLATE-FIG. 5). Free-hand cross-sections of both branches and branchlets of this and over a dozen other species were stained in aniline blue and mounted in glycerine for study; some cleared whole-mounts of stems were also studied. The structure in *P. reticulatus* will be explained first and then the other species will be compared with it.

The nodes of *P. reticulatus* (PLATE-FIG. 6) are trilacunar with a single trace from each leaf-gap. The same structure is developed in all other species investigated, although the configuration of the traces varies somewhat depending on the size of the foliar parts. In *Phyllanthus*, as in most Euphorbiaceae, the two lateral traces supply the stipules and only the central trace enters the base of the petiole. In species such as *P. acidus*, which have small, delicate stipules the stipular traces are so small that in a slightly oblique free-hand section of the nodal region the node may appear unilacunar. In species with relatively massive stipules such as *P. maleolens*, however, the stipular traces are large and conspicuous (PLATE-FIG. 7).

The epidermis of the young stem of *P. reticulatus* is composed of small chlorophyll-less cells with slightly convex outer walls covered by a thin cuticle; rarely, occasional cells are tanniferous. In other species, such as *P. shaferi*, *P. subcarnosus*, and *P. maleolens*, the cuticle is considerably thickened. In all species examined, the stomata are nearly plane with the surface of the epidermis, or at least are not distinctly sunken. In both the stem and branchlet of *P. reticulatus* there is a distinct hypodermis which is usually one cell thick and composed entirely of tanniferous cells. The term "hypodermis" is here used in the noncommittal topographical sense of Solereder (1908: 1076-1077), as developmental studies are still required to establish whether it is a true hypodermis or a double epidermis which is developed in *Phyllanthus*. In *P. acidus*, *P. emblica*, and *P. discolor* there is no differentiated hypodermis, while in *P. subcarnosus* it is well-defined.

In the branchlet of *P. reticulatus* the remainder of the cortex is composed of unspecialized parenchyma cells; but in the stem, where the cortex is much thicker, there are quite a number of tanniniferous cells (some of them aligned in more or less discontinuous rows which roughly parallel the hypodermis) and the cell-layers immediately beneath the hypodermis are formed of collenchyma. Conspicuous tannin cells were also observed in the cortex of *P. emblica* and *P. maleolens*, while in the material examined of *P. subcarnosus* and *P. acidus* tannin is lacking. *Phyllanthus shaferi*, *P. incrustatus*, and *P. maleolens* have stone cells in the cortex, and the first two species have rhombic crystals as well.

In *P. reticulatus* the primary phloem ("pericycle") fibers are thin-walled and occur as near-contiguous caps separated by the phloem rays. The other species of *Phyllanthus*, and those investigated by Froembling, also had primary phloem fibers occurring in discontinuous groups, although some had elements with thicker walls. The phloem parenchyma in *P. reticulatus* stands out in cross-section because of the abundance of longitudinally elongated tanniniferous cells.

All the species investigated had relatively thin-walled primary and secondary xylem elements; and nothing was seen suggesting the condition reported by Pax (1884: 399; pl. 6, fig. 10), who claimed that the xylem nearest the pith was in the *Phyllanthaceae* composed entirely of extremely thick-walled "Tracheiden" [fibers?]. Although Pax (l.c.) qualified his statement by saying that the condition was poorly developed in a number of species of *Phyllanthus* and *Breynia*, it is probable that he was mistaken as to the nature of the cells concerned. Rothdauscher (1896) reported no such "primary" elements in his detailed examination of the *Phyllanthaceae*. Probably the cells in question are lignified pith cells, which Rothdauscher (1896: 18, 86) reported for the majority of the *Phyllanthaceae*, including *Hemicyclia*, the genus Pax used for his illustration.

The pith of *P. reticulatus* consists of parenchyma cells with unlignified walls; those of the branchlet appear to lack contents but those in the stem may contain crystals or tannin. Tannin was also observed in the pith in *P. abnormis*, *P. cladanthus*, and *P. emblica*. Conspicuous formation of starch in the pith was seen only in *P. acidus*. *Phyllanthus shaferi* has rhombic crystals in the pith, while *P. incrustatus* is the only species investigated showing stone cells in both pith and cortex. Lignification of the walls of the pith cells was observed only in *P. maleolens*; but in *P. discolor* and *P. montanus* the walls have a striking appearance due to the conspicuous primary pit fields. These are enlarged, more or less elongated, and may be appressed side-by-side so that the entire wall has scalariform pitting like that between vessels and ray parenchyma cells. Metcalfe and Chalk (1950: 1228) report medullary bundles in *Phyllanthus*, but examination of the West Indian material and of the literature has failed to suggest any basis for their statement.

The mature stem structure may now be surveyed, beginning with the periderm. Cork formation is mainly subepidermal, as reported by Froembling (1896: 71); the single species mentioned by him as forming cork

within the pericycle, *P. obovatus*, is really a species of *Glochidion*. Gaucher (1902: 171) found that in *P. welwitschianus* the cork cambium develops in the second or third sub-epidermal layer. *Phyllanthus incrustatus*, and a few other West Indian species, have a precocious and excessive amount of cork production which results in the breaking up of the epidermis (and perhaps one or two outer layers of the cortex) into plates; the stems of these species consequently have the curious appearance of being incrustated with bran-like flakes (PLATE-FIG. 8). Unusually specialized cells were not encountered in the cork of most species, although a few sclerenchyma cells were noted along the inner edge of the cork in *P. emblica*.

Pax (1884: 413) reported that sclerenchyma was formed only in the primary phloem in the Phyllanthaceae, but Froembling (1896: 71) and Rothdauscher (1896: 22) found secondary "Hartbast" present in both the Euphyllanthaceae and the remainder of the Phyllanthaceae. Froembling noted that these secondary elements, which could be distinguished from the primary ones by their different color and greater diameter, occurred in the secondary phloem of a number of species of *Phyllanthus*, including the West Indian *P. ovatus* and *P. nutans*. Among the Harvard material, secondary fibers of this sort were observed in *P. emblica*. In *Phyllanthus*, as in other genera of the Phyllanthaceae, this secondary phloem sclerenchyma is scanty and does not form definite layers. Whether this breaks down the supposed distinction of the Phyllanthaceae from the Brideliaceae, which are reported to have distinct layering of parenchyma and sclerenchyma in the phloem, remains to be seen.

Stone cells were reported in the phloem of *P. multilocularis* and *P. helferi* by Froembling, but these two species actually belong in *Glochidion*. No stone cells have as yet been detected in the phloem of *Phyllanthus*, although they probably occur. Froembling also noted many small druses borne in septate fibers ("Krystalkammerfasern") in the phloem of most species of *Phyllanthus* and reported styloids in several, as well as compound ("zusammengesetzte") crystals in the form of a "W" in *P. wightianus*. In the Harvard material, styloids were observed in the chambers of elongated, septate, thick-walled cells in the phloem of *P. emblica*. But these cells, the "Krystalkammerfasern" of Froembling, are not lignified as are the septate fibers in the wood.

The structure of the xylem of *Phyllanthus* is much better known than that of the phloem. The following account is based on personal observations and on data from Froembling (1896), Janssonius (1930), Pearson and Brown (1932), and Metcalfe and Chalk (1950). The descriptive terminology is based on the standard definitions as presented by Moseley and Beeks (1955) in their comparative analysis of the xylem of the Garryaceae. An important qualification which should be kept in mind is that the majority of species of *Phyllanthus* are not truly arboreal, and many of the shrubby species have very slender stems. Consequently, the amount of secondary xylem of many species will be inadequate for comparisons between mature and young wood or between woods of different species.

The tracheary elements in the xylem of *Phyllanthus* are vessels and libriform fibres. In cross section (PLATE-FIG. 9) the vessels appear mostly solitary or in groups of two or three, although Janssonius reports radial groups of up to eight in *P. emblica*. Vessel diameter is very small. In the four species on which measurements (of one hundred for each species) were made, the range and mean diameters were found to be as follows: *P. emblica* 52–99 μ , mean 75.6 μ ; *P. botryanthus* 23–58 μ , mean 40.2 μ ; *P. incrustatus* 20–47.5 μ , mean 35.4 μ ; and *P. orbicularis* 20–44 μ , mean 30.3 μ .

Pearson and Brown and Janssonius reported 13–25 vessels per square mm. in *P. emblica*, but in the Harvard material the average was 53 per square mm., "very numerous." Apparently this species, which has ill-defined growth rings, is quite variable in density of vessels. *Phyllanthus botryanthus*, which is believed to be a rather primitive species on the basis of its growth form, shows this anatomically in its extremely numerous small vessels which average about 97 per square mm.! Examination of additional species is desirable, in order to determine whether this high vessel density is general throughout the genus.

As reported in the literature, all species examined have vessel-elements with simple perforations, but the end-walls of the vessel-elements are usually quite oblique (PLATE-FIG. 12). Inter-vascular pitting is alternate and small, while pitting to ray or xylem parenchyma cells is simple or narrowly bordered with larger pits that are often transversely elongated or even scalariform.

As may be seen from TABLE 1, the vessel-elements of *Phyllanthus* fit neatly into the "medium-sized" class, the mean lengths falling within the 350–800 μ range. There is no apparent correlation between vessel-element length and taxonomic position, at least on the basis of the relatively few species so far investigated.

The xylem fibers of *Phyllanthus* are ordinarily septate and have very small inter-fiber pits with linear orifices (PLATE-FIG. 13). They vary in total length from about 350 μ ("very short") to about 1700 μ ("moderately long"), with the mean lengths of 700–1100 μ covering the "moderately short" range. The mean fiber length appears to be a much better indicator of degree of specialization and of systematic position than does the mean vessel-element length, but the correlation is far from exact. *P. pachystylus* and *P. microdictyus*, two of the most primitive species examined, do have long fibers averaging 992 and 1003 μ respectively, while those of the highly specialized *P. orbicularis* and *P. epiphyllanthus* average 700 and 731 μ . But *P. chryseus*, which is also a highly evolved species, has the longest fibers of the species studied, the mean falling at 1098 μ . The data as a whole, nevertheless, are suggestive enough to warrant a much more extensive survey of the lengths of imperforate tracheary elements within the genus.

Xylem parenchyma in *Phyllanthus* is mostly paratracheal and scanty, one or a few cells commonly occurring adjacent to a vessel and often between a vessel and a ray. As Pearson and Brown stated, there is also very

scanty metatracheal parenchyma in *P. emblica*, diffused among the fibers. Janssonius reports that the xylem parenchyma strands in *P. emblica* are up to six cells high, and the pit-pairs to vessel elements either simple or half-bordered.

TABLE I

LENGTH OF TRACHEARY ELEMENTS *

Species	Range of fiber length	Mean fiber length	Range of vessel element length	Mean vessel element length
<i>P. pachystylus</i> (Webster 3906)	577–4150 μ	992 μ	202–974 μ	477 μ
<i>P. microdictyus</i> (Webster 3809)	607–1480	1003	368–932	638
<i>P. incrustatus</i> (Webster 4014)	444–1243	993	340–1021	761
<i>P. orbicularis</i> (Webster 3884)	383–1406	700	281–696	474
<i>P. epiphyllanthus</i> (Jervis 1368)	370–1510	731	168–706	429
<i>P. subcarnosus</i> (Webster 4683)	400–1566	936	330–765	600
<i>P. chryseus</i> (Webster 3853)	661–1723	1098	296–1479	702

* All measurements are in microns, on the basis of 100 fibers measured for each species; total numbers of vessels measured varies as follows: *P. pachystylus* 100; *P. microdictyus* 40; *P. incrustatus* and *P. orbicularis* 50; *P. subcarnosus* 60; *P. chryseus* and *P. epiphyllanthus* 100.

The rays in the two species of *Phyllanthus* studied from radial and tangential sections are so different that they must be described separately. As reported by Janssonius and by Pearson and Brown, only multiseriate rays are present in the xylem of *P. emblica*. These rays in tangential section appear composed of roundish cells, with uniseriate wings absent or rudimentary. In the classification of Kribs (1935), the rays therefore fall into the category Homogeneous II (PLATE-FIG. 10). The rays in *P. botryanthus*, on the other hand, clearly belong in the class Heterogeneous IIA: the multiseriate rays have long uniseriate wings, the uniseriate rays are abundant and well-developed, and transitional forms between the two types are rare (PLATE-FIG. 11).

The rays of *P. emblica* and *P. botryanthus* differ quantitatively as well as qualitatively. The multiseriate rays of *P. emblica* are greatly elongated vertically, some of them hundreds of cells and over 5000 μ high; transversely, they are 2–9-seriate and up to 190 μ wide. These massive rays occupy such an appreciable bulk of the wood that there are only 3–5 of

them per mm. In contrast, the multiseriate rays of *P. botryanthus* are mostly only 15–40 cells high (extremes 10–80, including the wings) and 2–5-seriate, with conspicuous uniseriate wings of 5–15 cells; they are so much less bulky that there are about 14 rays per mm. (including the uniseriate). The uniseriate rays of *P. botryanthus*, which consist of vertically elongated cells quite unlike the roundish ones making up the bulk of the multiseriate rays, are mostly 4–10 cells high but sometimes up to 20. In the rays of both species are some cells containing tannin and others with rhombic crystals of calcium oxalate.

The striking differences in ray structure between these two species is an indication that further investigation within the genus might provide taxonomically significant results. Section *Emblica*, to which *P. emblica* belongs, has at various times been recognized as a genus distinct from *Phyllanthus*. The validity of this and other generic segregates may ultimately be decided partly on the basis of such evidence from wood anatomy.

The difference in the rays of *P. emblica* and *P. botryanthus* assumes additional significance when the affinities of the fossil woods assigned to the form-genus *Paraphyllanthoxylon* are considered. As established by Bailey (1924) on the basis of Cretaceous petrifications from Arizona, the genus was characterized by scanty paratracheal parenchyma, vessel-elements with simple perforations, septate fibers, and mostly multiseriate rays with 1–5 elongated marginal cells. The rays are thus more or less intermediate between those of *P. emblica* and those of *P. botryanthus*. It is quite possible that *Paraphyllanthoxylon arizonense* belongs to one of the genera of Phyllanthinae, and it may prove to represent a species of *Phyllanthus* of an extant section when the xylem structure of the genus is better known.*

The detailed anatomy of the species of *Phyllanthus* in which the stems are modified into phylloclades will be discussed in another place, where extended analyses of individual species can be given. Here the purpose is to indicate in a general way how the phylloclades compare anatomically with the less specialized kinds of stems. As Dingler suggested, an independent evolution of phylloclades appears to have occurred in the South American and West Indian species which were all placed by Mueller in sect. *Xylophylla*. Consequently, the South American plants should be associated with *P. choretroides* in sect. *Choretropsis*, and sect. *Xylophylla* should be restricted to include only the West Indian species. Dingler also contributed the interesting suggestion that the phylloclades of the two groups could be distinguished in a general way on the basis of their respective patterns of development. In the phylloclades of sect. *Xylophylla*, it is the cortex which undergoes the most intensive growth to make up the bulk of the mature structure, while in sect. *Choretropsis* the cortex remains thin and a larger volume is occupied by the pith. A corollary of this is

* Since this paper went to press, examination of additional material (kindly loaned from the Yale slide collection by Dr. William Stern) has shown that in *P. acuminatus* the ray structure is more or less intermediate between that of *P. emblica* and *P. botryanthus*, and thus approaches *Paraphyllanthoxylon*.

that in sect. *Xylophylla* the vascular cylinder tends to break up into several closed bundles and thus produce a polystelic appearance, whereas in sect. *Choretropsis* the stele merely becomes greatly flattened.

The compound phylloclade of the commonly cultivated "greenhouse" *Phyllanthus*, *P. × elongatus*, shows in cross-section a structure more or less characteristic for all the species of sect. *Xylophylla*. In both the penultimate (PLATE-FIG. 14) and ultimate (PLATE-FIG. 15) axis there is a layer of chlorophyll-less hypoderm underlying the rather thickly cutinized epidermis. The outer cortex is composed of chlorenchyma which is not clearly differentiated into either palisade or spongy mesophyll, while the inner cortex resembles the pith. The numerous cortical bundles of thick-walled fibers appear mostly to be independent of the vascular tissue, as reported by Dingler (1885: 36), although they are structurally similar to the fibers of the primary phloem bundles and may sometimes be derived from these. The chief difference between the penultimate and ultimate axis is in the stele, which is intact, although flattened, in the penultimate axis but is broken up into concentric bundles in the ultimate axis so that a polystelic appearance results. The simple phylloclade of *P. epiphyllanthus* (PLATE-FIG. 16) anatomically resembles the ultimate axis of the phylloclade of *P. elongatus*.

The simple phylloclade of *P. montanus* (PLATE-FIG. 17) differs from those of the other West Indian species anatomically as well as in its more leaf-like outer form. The mesophyll is organized into a very dense palisade layer encircling the phylloclade just within the hypodermis, so that the structure appears that of a "centric" leaf-blade. But the greatest difference is in the stele, which is flattened and somewhat dissected but with the xylem masses on the abaxial and adaxial sides facing one another; no concentric bundles are formed. The phylloclade of *P. montanus* therefore resembles the penultimate axis of the phylloclade of *P. elongatus*. In this respect it resembles the phylloclades of the South American species of sect. *Choretropsis*, but this must be regarded merely as an interesting case of convergent evolution.

(To be continued)

THE AMAZON INDIAN AND EVOLUTION IN *HEVEA*
AND RELATED GENERARICHARD EVANS SCHULTES¹*With four plates*

I.

TO-DAY the genus *Hevea* is one of the most important groups of plants to civilised man, for it is the source of an overwhelmingly large part of his natural rubber. Despite the fact that rubber is indispensable to modern civilisation, it is wholly possible that the earliest use man made of *Hevea* was merely as a source of food. Even now, the Indian who lives in the murky corners of the Amazon forest has little use indeed for the rubber-bearing latex of the tree. Nevertheless, the seeds of various species of *Hevea* are, in season, a regular and esteemed article of diet amongst many tribes of the northwest Amazon.

It is meet that a thorough study of the role of *Hevea* as a food be made. The subject is of intense ethnobotanical interest in itself, but there is yet a more compelling reason for examining this relationship between man and rubber trees. A recent series of thought-provoking articles (1, 2, 4, 10, 40, 41) implies that this curious relationship has acted as a catalytic factor in certain phases of the evolution of the genus. Far-reaching conclusions have been drawn. Some of these conclusions call for objective examination, lest they become so intricately elaborated, so confounded and so widely accepted that their critical evaluation turns out to be a much more difficult task.

In this paper, I propose 1) to review what we know of the history of the utilisation of *Hevea* as a food; 2) to discuss my own observations of this particular use of the rubber² tree in the northwestern part of the Amazon Basin; and 3) to evaluate the recently proposed hypotheses as to how this use may have affected evolution in *Hevea*.

There is a group of related genera in the Euphorbiaceae to which *Hevea* is usually assigned: the *Hevea-Micrandra-Vaupesia-Joannesia* complex. Forasmuch as the seeds of several species of *Micrandra* and *Vaupesia* are used by Indians in an identical way as a food, our discussion will necessarily include these genera. We would be warranted in assuming, I believe, that whatever evolutionary influence this use may have had in *Hevea*

¹ Curator, Orchid Herbarium of Oakes Ames, Botanical Museum of Harvard University. The field studies upon which I have drawn for the data published in this paper were carried out whilst I was serving the Rubber Plant Investigations, Bureau of Plant Industry, United States Department of Agriculture as botanist, entrusted with jungle exploration for representative and elite trees of *Hevea* and related genera for the cooperative *Hevea* Rubber Development Program in Latin America (22).

² In this paper, I use the term "rubber" or "rubber tree" to refer only to *Hevea*, and to refer to all species of *Hevea*, not merely the commercially important species, *H. brasiliensis*; the term *cumuri* refers to *Micrandra Spruceana*.

could be paralleled in the case of related genera growing in the same area and habitats. No discussion of *Joannesia* is needed, for its seeds have never been reported as a food.

II.

Preliminary to a discussion of any phase of evolution in these groups, a short summary of the genera in question would seem to be in order, especially so since there has been so much difference of opinion in the past in regard to their classification.

HEVEA Aublet

Described in 1775 by Aublet (3) from material collected in French Guiana, *Hevea* is by far our most important genus of rubber yielding plants. It is the source of more than ninety-five percent of the world's natural rubber, and most of this amount is produced by a single species: *Hevea brasiliensis*. The genus is native to South America, where it is

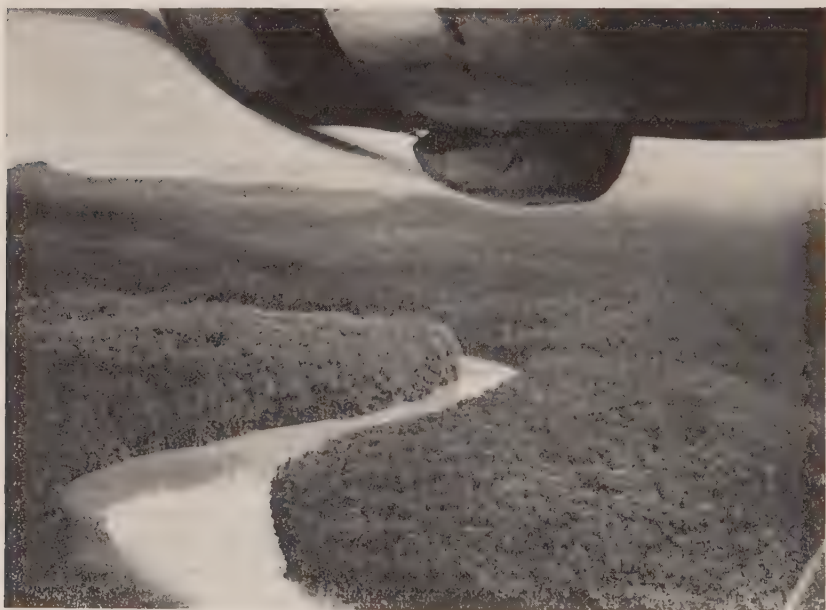


FIGURE 1. Aerial view of the forests of the Río Apaporis below the Falls of Jirijirimo, Colombia. The great massif of the Cretaceous, quartzitic Mount Isibukuri can be seen in the background. Much of the topography of the north-west Amazon (the basins of the Río Negro and Río Caquetá) is of this rolling type with large areas which, unlike the eastern and central parts of the Amazon Valley, are never subjected to flooding. On this high, rolling hinterland the abundant species of *Hevea* are *H. guianensis*, *H. guianensis* var. *lutea*, *H. nitida*, and *H. pauciflora* var. *coriacea*.

known from the Amazon Valley, the upper Orinoco Valley, the Guianas and the Matto Grosso region of Brazil. Highly typical of the Amazonian "hylaea" (16), *Hevea* exhibits much morphological variability and chooses a wide range of ecological sites. Its members range from forest giants to shrubby, sometimes almost prostrate, treelets and are found growing in deeply flooded alluvial land, in acidic boggy sites, on high well-drained upland and on the tops of xerophytic quartzitic mountains. As in many groups of tropical trees, natural variability has led, in the past, to the description of too many specific concepts. At one time, specialists held that the genus comprised twenty or more species (18, 19, 21), but recent workers are in essential agreement that there are only eight or nine (4, 11, 13, 14, 31, 32, 33, 40, 41). Trees of *Hevea* are usually called *seringa* or *siringa* in Brazil, Colombia and Venezuela, *shiringa* or *jebe* in Peru and Bolivia.

1. *Hevea Benthamiana* Mueller-Argoviensis in Linnaea 34: 204. 1865.

An inhabitant of low alluvial flood-sites and often-times growing in all-year *Mauritia*-bogs, *Hevea Benthamiana* is one of the most distinct of the species. It occurs only north of the Amazon River in the northwestern part of the Amazon Valley and the upper Orinoco. It is especially abundant in the Rio Negro basin. It may reach a height of ninety feet but usually is a medium-sized tree. A yielder of rubber only slightly inferior to that of *Hevea brasiliensis*, *H. Benthamiana* is often tapped commercially, but it has never been used for plantation stock. Its latex is pure white. *Hevea Benthamiana* is easily recognised by the golden-brown indument on the under surface of its leaves. There appears to be comparatively little variability in this species in the undisturbed forest.

2. *Hevea brasiliensis* (Willd. ex Adr. de Juss.) Mueller-Argoviensis in Linnaea 34: 204. 1865.

With the exception of one small area west of Manáos, *Hevea brasiliensis* is apparently confined to areas in the Amazon Valley south of the Amazon River and to the Matto Grosso and Paraná (14). In most parts of the Amazon Valley, it is usually associated with periodically-flooded areas, but in the Matto Grosso of Brazil, in Bolivia and in the Madre de Dios in Peru, it abounds on high, well-drained upland areas, where it becomes a much taller and more corpulent tree, attaining a height often of 130 feet. As the outstanding species from a commercial point of view, *Hevea brasiliensis* has received by far the greatest amount of botanical study in the field. Because of our fuller knowledge of this concept, some workers have thought *Hevea brasiliensis* to be the most variable of the species; in reality, it is no more variable — and probably less so — than most of the other species. Its latex varies from a pure white to cream-white.

3. *Hevea guianensis* Aublet Hist. Pl. Guian. Fr. 2: 871. 1775.

The most widespread of the species, *Hevea guianensis* is found throughout the range of the genus and shows much morphological variability. Its

great range and its variability may possibly indicate that *Hevea guianensis* is one of the oldest species of the genus. Even though its cream-yellow latex yields a rubber of inferior quality, the species, like its variety *lutea*, is assiduously tapped over a wide area, especially in eastern Colombia. At home on well-drained upland or on high river-banks which are subject to light flooding for only a short period, *Hevea guianensis* usually becomes a gigantic tree more than one hundred feet tall, often overtopping the jungle canopy. This species and its variety *lutea* may be distinguished at once by their conspicuously erect leaflets.

- 3a. *Hevea guianensis* Aublet var. *lutea* (Spruce ex Benth.) Ducke et R. E. Schultes in *Caldasia* 3: 249. 1945.

Almost as widely distributed as *Hevea guianensis* itself, this variety can sometimes be distinguished from *Hevea guianensis* by its very conspicuously obovate and abruptly apiculate leaflets, but both vegetative and floral characters separating the two often intergrade. The latex of *Hevea guianensis* var. *lutea* usually is more deeply yellow than is that of *H. guianensis*.

4. *Hevea microphylla* Ule in Engler Bot. Jahrb. 35: 669, t. 1, figs. j, k, l, m. 1905.

Without doubt the most distinct species of *Hevea*, *H. microphylla* appears to be a strict endemic of the uppermost Rio Negro basin in Brazil, Colombia and Venezuela (35). It demands low land which, flooded often to a depth of ten feet for four months during the rainy season, retains a boggy condition throughout the year. The tree has a conspicuous and characteristic swelling at the base and tapers rapidly to a slender, flexuous trunk, often reaching a height of sixty feet and supporting a very sparse crown. The pistillate flowers have an unusually well-developed torus. The capsules, with leathery instead of woody valves, are pyramidal and pointed. The fruit does not dehisce suddenly, shooting the seeds appreciable distances as in all other known species; on the contrary, it opens slowly and drops the seeds directly beneath the tree. The white latex is very watery and almost completely lacks rubber, for which reason it is never gathered by tappers. Until recently, this concept has been called *Hevea minor* Hemsley, a synonym of *H. pauciflora* var. *coriacea*.

5. *Hevea nitida* Martius ex Mueller-Argoviensis in Martius Fl. Bras. 11(2): 301. 1874.

Formerly known as *Hevea viridis* Huber, this species is one of the most interesting members of the genus. Usually a medium-sized tree with a sparse crown, growing in light caatinga-forest on sandy soil, *Hevea nitida* sometimes becomes, in areas of light inundation, a stout tree up to ninety feet in height. One of its distinguishing characters is the very shiny upper surface of the reclinate leaflets. Its thin, white latex is of no value as a source of rubber; indeed, if its latex be mixed (as has often happened when new jungle areas were opened to tapping) with that of *Hevea Benthiana* or

H. guianensis, it acts as an anti-coagulant (24, 28). The rather disrupted distribution of *Hevea nitida* includes almost the whole Amazon Valley and the uppermost Orinoco, but the species seems to be most abundantly developed in the Rio Negro basin of Brazil and in Amazonian Colombia.

- 5a. *Hevea nitida* Martius ex Mueller-Argoviensis var. *toxicodendroides* (R. E. Schult. et Vinton) R. E. Schultes in Bot. Mus. Leaflet, Harvard Univ. 13: 11. 1947.

A bushy treelet, usually not much exceeding eight feet in height, *Hevea nitida* var. *toxicodendroides* is known only from the isolated, remnant, quartzitic mountains of Cretaceous age in eastern Colombia (24, 26, 28). Here, occurring on sandstone which is almost devoid of soil, the treelet grows under severe conditions of psammophytic and chersophytic drought. Nevertheless, specimens which have been planted in rich alluvial soil at Urabá, Colombia, under excessive rainfall, retain their bushy habit of growth. Unlike that of *Hevea nitida*, the latex of this variety has a relatively high percentage of caoutchouc.

6. *Hevea pauciflora* (Spruce ex Benth.) Mueller-Argoviensis in Linnaea 34: 203. 1865.

Hevea pauciflora, known from the Rio Negro and upper Orinoco basins and from the Guianas, is not nearly so widespread nor abundant as is its variety *coriacea*. It is a rather corpulent tree with large, membranaceous (except in age) leaflets and very large seeds. The latex is white and has a low caoutchouc and high resin content.

- 6a. *Hevea pauciflora* (Spruce ex Benth.) Mueller-Argoviensis var. *coriacea* Ducke in Arch. Inst. Biol. Veg. Rio 239. Jan. 2, 1935.

Like *Hevea nitida*, with which it sometimes grows, this variety has a rather wide but disrupted range (15, 37). It is a small to medium-sized tree, seldom surpassing sixty feet in height, growing on rocky hillsides or high river-banks which are well drained and safe from the annual flood. The latex of *Hevea pauciflora* var. *coriacea* varies from whitish to a tawny yellow; it is never a pure white, as in the species. The leaflets, which are usually smaller than in the species, have a leathery texture from a few weeks after their appearance and become very thick-coriaceous, often somewhat marginate, in age. The seeds are very small to medium-sized.

7. *Hevea rigidifolia* (Spruce ex Benth.) Mueller-Argoviensis in Linnaea 34: 203. 1865.

A strict endemic confined apparently to the uppermost Rio Negro basin of Brazil, Colombia and Venezuela, *Hevea rigidifolia*, like *H. pauciflora* var. *coriacea*, with which it often grows, prefers high, well-drained, sandy or friable soil supporting a light caatinga-forest. It is commonly a medium-sized tree, sixty feet in height, with a sparse crown. The latex, which usually has a slightly cream-yellow hue, is poor in rubber and high in resin.

An outstanding characteristic of *Hevea rigidifolia* lies in the extremely thick-coriaceous and very strongly revolute-marginate leaflets which are always borne in a conspicuously reclinate position.

8. *Hevea Spruceana* (Benth.) Mueller-Argoviensis in *Linnaea* 34: 204. 1865.

Hevea Spruceana occurs in great abundance on low and very deeply flooded river-banks along the Amazon River itself from its mouth up to about its confluence with the Iça or Putumayo and along the lower courses of the tributaries of the lower Amazon. The trunk is conspicuously bellied at the base, and the tree has leaflets which are usually more or less densely velutinous on the under surface. The flowers seem almost never to be yellow, usually varying between a purplish brown and brown colour, and are sometimes objectionably pungent-aromatic. As its watery, white latex is almost devoid of rubber, *Hevea Spruceana* has no commercial interest to the tappers. The capsule and seeds are the largest of the genus.

MICRANDRA Bentham

Micrandra (including those species formerly accommodated in *Cunuria*) comprises some 13 species, all confined to South America (36). The genus is probably rather closely allied to *Hevea*, but it has a much wider range. Known from the entire Amazon basin and from southeastern Brazil, the Orinoco drainage-area and all of southern Venezuela, the Guianas, as well as from the Magdalena Valley in Colombia, *Micrandra* would appear to be an old genus. Only one species — *Micrandra minor* — has been of any commercial importance as a rubber producer. As in *Hevea*, the species of *Micrandra* exhibit a predilection for a wide range of ecological sites, from river-banks to mountain-slopes and from areas of heavy to light rainfall, but none is known to prefer the permanently boggy sites chosen by some of the species of *Hevea*.

In Brazil and Colombia, certain species of *Micrandra* are known as *arara-siringa* or *cunuri*.

1. *Micrandra australis* (R. E. Schult. ex Baldw. et Schult.) R. E. Schultes in *Bot. Mus. Leafl. Harvard Univ.* 15: 202. 1952.

Micrandra australis is a poorly understood species known from a high plateau between two tributaries of the Rio Madeira in the central part of the Amazon basin.

2. *Micrandra bracteosa* Mueller-Argoviensis in *Martius Fl. Bras.* 11(2): 290. 1874.

This species is very incompletely understood. Known only from several very old collections, it seems to be confined to coastal Brazil (Bahia).

3. *Micrandra brownsbergensis* Lanjouw *Euph. Surinam*, 34, *tt.* 7, 8. 1931.

A medium-sized tree occurring in the lowland rain-forests of Dutch and French Guianas.

4. *Micrandra elata* (Didrichs) Mueller-Argoviensis in *Linnaea* 34: 142. 1865.

Micrandra elata is an apparently rare tree of medium-size known only from southeastern Brazil (Minas Gerais and São Paulo). It is the southeasternmost representative of the genus.

5. *Micrandra glabra* (R. E. Schult. ex Baldw. et Schult.) R. E. Schultes in *Bot. Mus. Leaflet*. Harvard Univ. 15: 203. 1952.

A seventy-five to one hundred foot tree, this species is known from British and Dutch Guianas and from Venezuela. It grows apparently in savannah forests associated with the ancient Venezuela-Guiana land-mass.

6. *Micrandra Gleasoniana* (Croiz.) R. E. Schultes in *Bot. Mus. Leaflet*. Harvard Univ. 15: 203, *t.* 65. 1952.

A tree up to sixty feet in height, known only from the Mazaruni drainage-area in British Guiana, where it appears to be associated with outcrops of the Venezuela-Guiana land-mass, *Micrandra Gleasoniana* is most conspicuous because of the dense yellowish, velvety indument on the under surface of the leaves.

7. *Micrandra Lopezii* R. E. Schultes in *Bot. Mus. Leaflet*. Harvard Univ. 15: 204, *tt.* 66, 67. 1952.

Micrandra Lopezii, a small tree of some forty-five feet in height, is a very strict endemic known only from several stations in the uppermost Rio Negro basin of Brazil and Colombia. It inhabits sandy caatingas where the forest is very light. It is apparently allied most closely to *Micrandra glabra*. The seeds are small for the genus. *Micrandra Lopezii* has an unbuttressed trunk, but there is a variant with well developed prop-roots: *M. Lopezii* var. *anteridifera* R. E. Schult.

8. *Micrandra minor* Benthams in Hooker Bot. Journ. 6: 372. 1854.

Widespread and abundant in the Amazon Valley and the upper Orinoco basin, *Micrandra minor* is a gigantic tree, often attaining a height of one hundred and ten feet. The crown is very heavy, and the corpulent trunk is unbuttressed. This species prefers high river-banks which are inundated only at the height of the annual flood, and is never found in low-lying swampy areas. The very abundant, thick, pure white latex yields a rubber of high quality and has been tapped in the past for "Caurá rubber"; but, as the tree cannot be subjected to repeated and frequent tapping, it is not promising for planting. *Micrandra minor* superficially resembles *M. siphonioides*, and the two concepts have sometimes been thought to be identical. *Micrandra minor* never has buttresses, whereas *M. siphonioides* always has enormous tabular roots. The former species is a riparian tree,

whereas the latter always grows on sandy, well-drained upland soil. In the nerve axils, on the under side of the leaf of *Micrandra siphonioides*, there are dense tufts of yellowish hair, but the leaf of *M. minor* is wholly glabrous. The natives distinguish between the two, calling *Micrandra minor* by the Brazilian name *arara-siringa* and referring to *M. siphonioides* as *arara-siringa da caatinga*.

9. ***Micrandra Rossiana*** R. E. Schultes in Bot. Mus. Leaflet. Harvard Univ. 15: 211, *tt.* 68, 69. 1952.

Micrandra Rossiana has a widespread, though very disrupted, range in the northwestern part of the Amazon Valley in Brazil, Colombia and Venezuela, occurring always on high knolls far above the annual flood. It is especially abundant in the Vaupés of Colombia. With no appreciable flow of latex, this species is an unbuttressed tree up to about seventy feet in height. The prominently carunculate seeds are relatively large.

10. ***Micrandra santanderiensis*** Croizat in Journ. Arnold Arb. 24: 169. 1943.

Obviously allied to *Micrandra brownsbergensis* and *M. elata*, this species is remarkable because of its distribution. The only species known west of the Andes, it occurs in the Magdalena drainage-area of Colombia.

11. ***Micrandra siphonioides*** Benth in Hooker Kew Journ. 6: 371. 1854.

This heavily buttressed caatinga-tree is abundant, albeit disruptedly distributed, in the northwestern part of the Amazon Valley from Manaus westward, being especially abundant in the Rio Negro basin of Brazil and Colombia. It is a poor yielder of latex and is never tapped. Its closest ally is *Micrandra minor*, with which it has often been confused. The crown is extraordinarily extensive, and it usually fruits in profusion, shedding great quantities of a medium-sized seed.

12. ***Micrandra Spruceana*** (Baill.) R. E. Schultes in Bot. Mus. Leaflet. Harvard Univ. 15: 217. 1952.

Better known under the binomial *Cunuria Spruceana* Baillon, this species is widespread on high, well drained soil in the western half of the Amazon Valley and the uppermost Orinoco. It occurs in Brazil, Colombia, Peru and Venezuela. In the Rio Negro basin of Brazil and in much of Amazonian Colombia, it is excessively abundant. It is a corpulent, well buttressed tree sometimes reaching ninety or one hundred feet in height. The capsules are borne in great abundance and yield large, glossy, reddish brown seeds very rich in oil. The white latex is very sparse and resinous and is never gathered.

13. ***Micrandra Sprucei*** (Muell.-Arg.) R. E. Schultes in Bot. Mus. Leaflet. Harvard Univ. 15: 218, *tt.* 70, 71 (upper fig.), 72, 73. 1952.

One of the most abundant of the caatinga-trees of the northwestern Amazon, especially in the upper Rio Negro basin of Brazil, Colombia and Venezuela, *Micrandra Sprucei* was, for a century, known only from Spruce's type collection. It is better known as *Cunuria crassipes* Mueller-Argoviensis.

VAUPESIA R. E. Schultes

A monotypic genus which seems to stand phylogenetically between *Micrandra* and *Joannesia*, *Vaupesia* is unknown except in a very restricted part of the northwest Amazon, in the basins of the Apaporis and Vaupés Rivers of Colombia and Brazil (39). The one species inhabits rocky and sterile but well-watered sites usually alongside cataracts and rapids in the rivers, where there are either quartzitic or granitic outcrops.

1. *Vaupesia cataractarum* R. E. Schultes in Bot. Mus. Leaflet. Harvard Univ. 17: 27, t. 12, 14. 1955.

Vaupesia cataractarum grows in isolated pockets, but, where it occurs, it is found in great abundance. A corpulent tree attaining a height of eighty feet, this species is, in its foliage and fruits, so similar to *Micrandra Spruceana* that the Tukano Indians of the Vaupés River employ the same name for both. The tree fruits profusely, each capsule containing three large, dull brown seeds. It is of no value as a latex-tree.

III.

Reports concerning the use of rubber seeds as food constituted merely curious ethnobotanical information until very recently. About a decade ago, these reports were taken up and, through a series of successively more far-reaching postulations, comestible use by primitive peoples of rubber seeds was credited with having had directly or indirectly really titanic influences upon the evolution of *Hevea*. So firmly entrenched have these postulations become in the literature in this short time that it behooves us to study them with an eye alert to their soundness. It will serve our purposes best, if the postulations be here quoted in the words of their proponents and as they were presented, from their prudent beginnings to their present strident positiveness.

In 1947, Baldwin (4) and Seibert (40) mentioned the fact that the Indians of the northwest Amazon eat *Hevea* seeds, and they utilised it as one argument in a series which they advanced to explain certain presumed steps in the evolutionary history of the genus.

Baldwin (4) assumed that, when forest is felled for house sites, the natives spare *Hevea* trees either because the trees are a source of latex "or, in some areas, because the seed are eaten, or because the wood is poor fuel." He pointed out that such a practice would present "excellent opportunities for hybrid swarms to become established." To the best of my knowledge, this is the first time that the primitive and probably earliest use

of *Hevea* has been considered thoughtfully from the point of view of what effect it might have had on the evolution of the genus.

Keenly interested in the phyletic significance of certain differences which he had observed in the loss of oil from seeds of a number of species of *Hevea*, Baldwin (7) has implied a correlation between oil content of the seed and their use as a food.

That seed of both *H. rigidifolia* and *H. Kunthiana* [usually known as *H. pauciflora*] lose oil in significant amounts suggests close genetic relationships between these species. Baldwin . . . stated that their seed are much alike and that the natives of the upper Rio Negro eat the seed of both species: he found a tree of *H. rigidifolia* that had been cut for its almost-mature seed and recorded that trees of *H. Kunthiana* are not uncommonly planted for their edible seed. Though the natives 'designate the latter tree *seringa*, they say it has seed like *cunury*.' Baldwin and Schultes . . . discussed the use of seed of *cunury* — i.e., of *Cunuria*, a genus with affinities to *Hevea* — as food of Amazonian Indians . . . And Baldwin . . . has mentioned the possibility of introgression between these genera. Pertinent here is the fact that *Cunuria* seed among my collections evidence no loss of oil. . . .

That the Amazonian native seems especially to select for food the seed of *H. rigidifolia* and of *H. Kunthiana* and that oil escapes freely from seed of these species are reasons for according this phase of the genus particular study.

Seibert (41) took this thesis further, arguing as follows:

Through its value as a food plant to the Indians of the Rio Negro region, it appears that *Hevea* became a semi-domesticated tree. Its domestication along the major waterways, in clearings, edges of villages and camp-sites followed a pattern of conscious or unconscious selection for seed production. The planting of certain species in the vicinity of other wild species substantially aided the process of interspecific hybridization. Once established in clearings, the mature hybrids and introgressive hybrids are (at least in part) capable of competing with the encroaching second growth. Several centuries of this slow process seem to have played a conspicuous part in the resultant hodge-podge of variables turning up as representative collections of *Hevea* from the Rio Negro. . . .³ From present evidence, it appears that *Hevea pauciflora* has been the species of *Hevea* most cultivated by the Indians of the Rio Negro and upper Amazon.

Under *Hevea pauciflora* (in which he included *H. pauciflora* var. *coriacea*), Seibert (40) went farther by saying that "in the hundreds of years Indians have been along the Rio Negro they have . . . distributed the species outside of its natural habitat." He entertains the possibility that *Hevea pauciflora* got as far as Iquitos, Perú, through the agency of man. "It would not be too hard," he argued (40) "to presume that *Hevea pauciflora* may have been introduced into Iquitos before the white man arrived."

³ There is a much greater development of speciation in *Hevea* in the northwest Amazon, but, on the basis of the available collections and on several years of field work along the Rio Negro and its western affluents, I venture to say that there is no greater variation here than in most other parts of the Amazon which are as well known. Certainly, so far as *Hevea* is concerned, there is no "hodge-podge of variables" in the area.

Seibert presented his postulations prudently, usually avoiding categorical statements. He undoubtedly hoped to stir up discussion and evaluation of his hypothesis. Unfortunately, there has developed a tendency recently to accept Seibert's suggestions *in toto* and to present them as well established and proven facts, with no inkling that they are highly hypothetical from beginning to end.

Anderson (1), for example, saw the problem as follows:

Apparently the species was first cultivated for its edible nuts . . . Either accidentally or with intent, seedlings from wild trees came up in clearings where they were being used for food. These areas were often outside the natural range of that species or variety and sometimes within pollination distance of other species. Consequently, these isolated trees tended to be cross-pollinated. Under the primitive agriculture of these areas, clearings were occupied for a time and then deserted. As the disturbed land gradually reverted to jungle, there were many opportunities for the hybrid seedlings of the isolated nut trees to germinate and survive. They crossed back to the native species of that vicinity, and thus the process of introgression might have started in hundreds of little clearings in the jungle. The more or less casual use of *Hevea* for its edible nuts increased the natural introgression between some of the species. When man gradually learned that the latex of *Hevea* also had its applications, he already had at hand variable, introgressed, semi-domesticated populations, in which trees superior in latex were more likely to be found.

More recently, Anderson (2) has taken the same theme to much bolder lengths, weaving into the story as previously elaborated additional and highly imaginative aspects. He states in part:

There is a great variation in the rubber content of the supposedly wild trees; some of the higher-yielding strains trace back to sites which are now part of the jungle but which indicate clearly that they had been village clearings before they were engulfed by the rapidly regenerating tropical brush . . . primitive man first domesticated the Pará rubber tree for its nuts . . . By doing this, they brought into their small and transient villages trees which were not just a random selection of the original wild species but just those with superior nuts, or a superior yield of nuts. In doing so, they frequently brought in trees which were not native to that immediate area . . . As these clearings were deserted, the alien trees crossed with those in the immediate vicinity and thus in more than one clearing there eventually developed mongrel swarms of Pará rubber trees, which had the heightened variability characteristic of mongrels. It was among them that some of our most potentially valuable breeding material was located when we eventually became much more interested in the milky sap than in the nuts.

In considering the "purity" of the *Hevea brasiliensis* material which was first imported into the Far East from Brazil, Dijkman (10) has cited some of Seibert's postulations in connexion with the use of *Hevea* seed as a food and has accepted as fact Seibert's thesis that the Indians spread *Hevea pauciflora* far and wide.

Seibert, in addition, has collected evidence of penetration of *H. pauciflora* into the *H. brasiliensis* complex referred to above. He assumes this probably first

began as a result of the natural enlargement of the original habitat; but the process seems to have been considerably hastened by the autochthonous inhabitants of the continent. The seed of this species and/or its expressions are eaten by the Indians, who carried the seed with them on their migrations and brought *H. pauciflora* under cultivation in their new settlements. . . . This man-caused spreading has created the impetus for its adaptation to a wide range of extreme climatic conditions.

Even a hasty review of the several passages which I have quoted above shows that an extraordinary amount of theoretical importance is being given to reports on the use of *Hevea* seeds as a food and far-reaching assumptions are being made in an attempt to build up a plausible sequence of events to fit into the hypotheses propounded. A moment's hesitation and thought will recommend caution and forbend unbridled play.

What, then, are the ethnobotanical facts, and how do these facts, bereft of unfounded trimmings, fit into the hypotheses which we have just reviewed?

IV.

Oddly enough, historical references give us very little information on the use of *Hevea*, *Micrandra* or *Vaupesia* seeds as a comestible. There may be several explanations for this. One reason which we must bear in mind is the paucity of reliable ethnobotanical records for the vast Amazonian forest area. Another may be the ease with which travellers could have overlooked this strange food, for the seeds of these jungle trees are normally available for but a very short time (about one month) each year and, as they do not keep, they must be used at once. It is hard to account for the dearth of references to this custom, even in the several detailed anthropological accounts of the Indians of the northwest Amazon written by men who had spent many months, even years, in the region. This silence in anthropological writings is all the less understandable when one realises that sometimes tribal festivals or dances are centered around the harvest of *seringa* or *cunuri* seeds for food.

To Fusée Aublet must go the credit of first reporting the use of rubber seeds as a food. In his description of *Hevea guianensis*, in 1775, he (3) wrote of certain Indians of French Guiana:

The Galibis [Caribs] and Garipons carefully gather the nuts from the fruits of this tree. They keep them and eat them with enjoyment. I have witnessed their assiduity in collecting the seeds when they come upon these trees on trips that I have made with them; I have imitated them. I have eaten many of these nuts without feeling any disturbance whatsoever.

This passage merits attention not only as the earliest report of this use of rubber seeds but also as the only report which apparently ignores their cyanic content. It is not easy to interpret Aublet's statement that the Indians "keep" the seeds, for they spoil with great rapidity. Furthermore, the seeds of *Hevea* and its allies *Micrandra* and *Vaupesia* are known to be

highly toxic to man, until the cyanic poisons are removed by long soaking or by boiling.

The next reference to the eating of *Hevea* seeds is that of the botanist Richard Spruce who spent seven years in the Amazon Valley and who, through his collecting, greatly advanced our knowledge of *Hevea* and its relatives. In 1854, Bentham (9) published Spruce's manuscript notes on *Hevea*, and we find the following report:

The seeds are an excellent bait for fish. Macaws eat them greedily, but to man and quadrupeds they are poisonous in a fresh state. The Indians on the Uaupés render them eatable in this way: after being boiled twenty-four hours, the liquor is strained off, and the mass that remains has something the colour and consistence of rice long boiled. Eaten along with fish it is exceedingly savoury.

It is of the utmost import here to make note that Spruce did not designate any *one* species of *Hevea* as a source of edible seeds. His discussion referred to the genus as a whole. There can be little doubt that Spruce meant that the Indians of the Vaupés River used any or all of the species as a source of comestible "nuts."

During my more than a decade of field work on *Hevea* and its relatives in the Amazon Valley, I have given critical attention to the part which these plants play in the economy and lore of the Indians, especially of the more primitive tribes which do not engage in rubber-tapping work.

The first observation which I must make is that, as far as the literature and my own observations attest, the seeds of *Hevea* and *Micrandra* are used regularly as an annual food exclusively in the northwestern part of the Amazon Valley — that is, in the basin of the Rio Negro in Brazil and in the Comisarias del Vaupés and Amazonas in Colombia. I have never heard reports amongst the inhabitants of other parts of the Amazon Valley, and botanists who have worked elsewhere tell me that they have not heard of the custom. Seibert, who spent a number of years in eastern Peru and who became extremely interested in Spruce's report of the food-use of rubber seeds, does not record it from any part of Peru. Dr. Adolpho Ducke, who has collected plants in all parts of the Amazon Valley for half a century, agrees that this aboriginal custom is peculiar to the northwest. One must needs, of course, distinguish between the regular and often ceremonial consumption of the seeds, on the one hand, and the occasional eating of them in isolated instances as a last resort during great famine, on the other hand.

The fundamental importance of this fact is at once evident. Restricted culture-trait that it is, the habit of eating rubber seeds could not have had the widespread effect postulated by Anderson and Dijkman. Baldwin realised that this use of the seeds was localised, but Seibert stated that it was a custom "within the Amazon Valley itself" and suggested man as an instrument of spread over great distances. Dijkman had the Indians carrying the seeds of *Hevea pauciflora* "with them on their migrations and brought *H. pauciflora* under cultivation in their new settlements," and he

speaks of "this man-caused spreading" as having helped adapt the species to a "wide range of extreme climatic conditions." Even were the custom of eating the seeds widespread, it would be impossible for Indians migrating any distance in open dugout canoes to carry along the notoriously short-lived rubber seeds in a viable state.

There is a second important observation which I must make. It is very probable that the seeds of all of the species of *Hevea* occurring in the northwest Amazon are eaten.

There would seem to have been a tendency to lay more stress on the importance of *Hevea pauciflora* as a source of food than on any other species. This must be examined critically, for there would seem likewise to be an implication that this species, partly because of its "cultivation" and "domestication" through man's interest in it as a source of food, has led to a great degree of intraspecific variation and has similarly caused this species to "penetrate" others and so influence markedly the course of development of the genus. Baldwin (4, 5, 7) reported that the natives of the upper Rio Negro select the seeds especially of *Hevea pauciflora* and *H. rigidifolia* for food; and Seibert (41) felt that the available evidence pointed to *H. pauciflora* as the species preferred.

There is no basis for the supposition that one or two species are preferred over others. In the northwest Amazon, all known species of *Hevea* but two — *H. brasiliensis* and *H. Spruceana* — are represented. Of the six species occurring in the region, the seeds of five of them are used as food. Whilst living in Indian sites in eastern Colombia, I have eaten the seeds from several species myself. Ducke (12) reported that the natives living along the Curicuriarí eat the seeds of more than one species of *Hevea*.

Hevea microphylla seeds, which are unusually large for the genus, do not seem to be gathered for food; and I think the reason for this is only the difficulty of harvesting them. *Hevea microphylla*, as we have seen above, grows in almost permanent bogs, and the *sarapó* and other fish, spawning in this season in the wake of the flooded forests, snap the seeds up with great alacrity. The capsules do not open with explosive violence, so the seeds are not shed in quantity, as in other species; when the capsule opens gently, the seeds fall one by one into the water below. The tiny seeds of *Hevea nitida* var. *toxicodendroides* are, apparently, never gathered for food because of their size.

If there be any rubber trees the seeds of which are more commonly used as food in the northwest Amazon, it is neither *Hevea pauciflora* nor *H. rigidifolia* but *Hevea guianensis* and *H. guianensis* var. *lutea*. This is due not to any preference but to the greater abundance and availability of these trees. I have seen collecting parties gathering the seeds of *Hevea guianensis* and its var. *lutea* amongst the Makunas of the lower Apaporis River, the Taiwanos of the Kananarí and the Kubeos of the Vaupés in Colombia. I have eaten mash from the seeds of *Hevea guianensis* in the country of the Kuripakos at the headwaters of the Guainía in Colombia. The Yukunas and Tanimukas of the Miritiparaná in Colombia make unleavened cakes from the seeds of *Hevea guianensis* var. *lutea* and of *Micrandra Spruceana*

as the principal starch food in their beautiful annual Dance of the Cunurí or Wě-ra. In this case, there seems to be a preference for seeds of *Hevea guianensis* var. *lutea* over those of *H. nitida*, even though, when the seeds are used as food in everyday life without any connexion with this semi-religious dance, both are used indiscriminately. There is probably some ceremonial reason for the choice, for the preference is a strict trait. The only "explanation" which I could get was that *Hevea guianensis* var. *lutea* is "cousin to" *Micrandra Spruceana*. Both tribes have distinctive names for these two rubbers: the Yukunas refer to *Hevea guianensis* var. *lutea* as *hě-che* (a name interestingly similar to that of *Micrandra Spruceana*: *yě-cha*) and to *H. nitida* as *ya-wá-ro*; the Tanimukas refer to the former as *wān-hoó-a*, to the latter as *wān-hoó-a-ma-ka-na*. The Miritiparaná is the only region in which I have found the mash or pulp from the seeds of either *Hevea* or *Micrandra* elaborated into cakes.

Hevea nitida is very widely employed in the northwest Amazon as the source of edible seeds. This tree, as we have seen, grows either in jungle which is but slightly flooded at seed-time or in upland forest on well-drained sand. Needless to say, it is usually the latter instead of the former habitat to which the Indians, in search of rubber seeds, repair. The reasons are clear. It is much more difficult to walk through a flooded forest, and the seeds are much less abundant because of the great quantities eaten by spawning fish. I have seen seeds of *Hevea nitida* gathered for food or eaten in Colombia by the Taiwanos and Kabuyaris of the Kananarí, the Tukanos, Desanos, Kubeos and Gwananos of the Vaupés, the Yukunas and Tanimukas of the Miritiparaná and, in Brazil, by the Tukanos of the Uaupés and Negro. Along the banks of the Vaupés River above Mitú, *Hevea guianensis* var. *lutea* and *H. nitida* often grow intermixed in the forests and, in this case, the Kubeos gather both indiscriminately, showing no preference for one over the other. This is likewise true amongst the Tukanos of the Tikié in Brazil.

I have not seen *Hevea Benthamiana* seed used, but the Kuripako Indians along the lower Guainía and a few Mirañas on the Caquetá in Colombia have informed me that this species may be used as a food, and Baldwin (5) reports its use on the Uaupés River of Brazil. It is easily understood why, in a region with highland species as well, *Hevea Benthamiana* would be neglected as a source of seeds: at harvest time, the rivers are at their highest, and *Hevea Benthamiana* stands in from three to ten feet of water.

There remain to discuss only *Hevea rigidifolia* and *H. pauciflora*, the two species which Baldwin suggested were the most important as a source of food-seed. *Hevea rigidifolia* is a comparatively localised species, but, as it grows in abundance in pockets of light forest on well-drained sandy soil, it is visited by the natives who live in its vicinity. It is eaten in quantity by the Tukanos and Desanos of that part of the Vaupés and Papurí Rivers which form the boundary between Brazil and Colombia. *Hevea pauciflora* seeds seem to be eaten mainly by the natives along the upper course of the Negro and the seeds of *H. pauciflora* var. *coriacea*,

not well liked because of their smaller size, are used in several areas along the Vaupés, Guainía and Apaporis Rivers in Colombia.

As pointed out above, the Indians along the main course of the Amazon River are not known to eat rubber seeds, unless conditions of famine prevail. It will be of interest here to record that I saw a group of Tikunas near Leticia, Colombia, prepare seeds of *Hevea brasiliensis* and eat the mash with baked fish. These Indians, who were engaged in collecting, under my direction, several tons of rubber seeds (27), had eaten all their fariña meal and were forced to turn to rubber seeds. They made it clear that these were only an emergency food. I mention this merely because I have not been able to find any reference on the edibility of the seeds of *Hevea brasiliensis*.

From the foregoing information, it ought to be clear that the seeds of most, if not all, species of *Hevea* can and are taken as food in the north-west Amazon.

It might be worthwhile here to look at the situation in *Micrandra* and *Vaupesia*.

Again we turn to Spruce for our earliest knowledge of *Micrandra* seed as a food. On labels of specimens of *cunuri* (*Micrandra Spruceana*) collected in the uppermost Rio Negro basin in 1853 and preserved at Kew, Spruce made the following annotation (8):

On the Uaupés and around São Gabriel [Estado do Amazonas, Rio Negro, Brazil], a large tree obviously allied to *Siphonia* [*Hevea*], called by the Indians *Cunuri*, is frequent in the forest. It has large arched buttresses at the base, like the *uacu* [*Monopteryx Uaucu* Spruce ex Benth.], from which it is distinguished by milk flowing from it when wounded. I have not yet seen its flowers or fruits, but the Indians describe the latter as tricoceous, quite as in *Siphonia*, and they use the seeds in a similar manner. These being boiled 24 hours yield a small quantity of oil, which serves for lamps. The pulpy mass into which the seeds have now fallen is packed in a basket and kept under water 3 days to sweeten; when taken out, it has a pleasant taste and no ill smell. It is eaten without the addition of anything else and may be kept a long time, but if the seeds have not been well boiled, it is a quick poison, and Indians have fallen victims to its incautious use.

In 1854, Spruce (19) reported that from the seeds of "*cunuri*, abundant on the alto Rio Negro, Orinoco, Casiquiare, Pacimoni, etc., the Indians prepare a paste resembling cream-cheese in appearance and taste. The seeds are first boiled and then steeped for some days under water, after which they are broken up by the hand. In the boiling, a quantity of oil is said to be collected . . . it is said to be as bitter as andiroba oil, but to afford an excellent light."

Apparently nothing more was written on *cunuri* seeds as food until recent years. Referring to *Micrandra Spruceana*, Ducke reported it for the Indians of the upper Rio Negro in 1934 (20). In 1943, Paul H. Allen (herbarium specimen *Allen 3063*) recorded a comparable use of *cunuri* by the Tukanoan Indians living on the Rio Papuri, an affluent of the

Vaupés and part of the boundary between Brazil and Colombia. In 1944, Baldwin found the seeds of *cunuri* eaten in the upper Rio Negro-Rio Vaupés region of Brazil (Baldwin et Schultes loc. cit. 344). And, in 1945, I (25) called attention to the use of *cunuri* seeds as food on the lower Caquetá and its affluents in Colombia:

The seeds of *Cunuria Spruceana* apparently contain a cyanide and, according to the natives, are extremely poisonous when taken internally in the crude state. The Indians of the lower Caquetá, however, consume quantities of the seeds in the form of a greyish mash which is prepared by boiling the pulp in three waters to remove the poison. This mash has a peculiar taste, somewhat like burnt potato. According to the natives, salt must not be added to this mash.

This was the first of many observations pointing to the value of *Micrandra Spruceana* as a food. Since then, I have witnessed the preparation of this food and have, on a number of occasions, partaken of it myself. *Micrandra* and *Hevea* fruit simultaneously. The seed of *Micrandra Spruceana* is much more highly esteemed than that of any other species of *Micrandra* and more than that of any *Hevea*, wherefore, if *Micrandra Spruceana* occurs in abundance in a given region, very little *Hevea* seed is gathered. *Micrandra Spruceana* grows on light sandy soil which never floods, the tree fruits prodigiously and the seeds are large and full of a firm pulp which handles easily in boiling. In former years, the oil which came to the surface during boiling was used in lamps, so that these seeds were rather valuable in the native economy.

According to reports which I have gleaned in the field, *cunuri* seeds are eaten by the Barasanas, Desanos, Gwananos, Kabuyaris, Karihonas, Kubeos, Kuripakos, Makunas, Miranas, Taiwanos, Tanimukas, Tatuyos, Tukanos and Yukunas in eastern Colombia. They are likewise used by some of the natives in the upper Rio Negro basin of Brazil and possibly also in the very uppermost Orinoco. I have witnessed the preparation and use of these seeds by the Karihonas, Yukunas and Tukanos. In all cases are the preparations similar: several boilings are always employed to remove the cyanic poisons.

Without a doubt, one of the most interesting ways of using *cunuri* seeds is the making of unleavened "bread" or casabe for the *Wě-ra* or Dance of the Cunuri of the Yukuna and Tanimuka Indians. A most beautiful dance, the *Wě-ra*, with the whole tribe participating, lasts for forty-eight hours. This dance takes place during the seeding-time of the *cunuri*, which is normally in March. Great groups of young men make ceremonial trips to areas of the forest where *Micrandra Spruceana* grows in abundance, large baskets are woven on the spot, and these are filled with seeds. Carried back to the house where the dance is to be held, the seeds are given over to the women who immediately start the process of boiling and washing out the poisons. The process is very similar to that used to prepare the meal or *fariña* from poison *Manihot*, and, indeed, it is the same or a similar poison which must be removed. After several boilings and washings, the damp mash is gently toasted on a flat plate over the fire and is reduced to a fine

greyish white meal. This is then made into *casabe* or unleavened bread, in much the same way as *fariña* (from *Manihot*) is used to make *casabe* cakes. Often the *cunuri* flour is, as pointed out above, mixed with flour from the seeds of *Hevea guianensis* var. *lutea*, but usually *Micrandra Spruceana* is used alone. The casabe cakes thus prepared are, together with smoked boar- or tapir-meat, the chief food of the dance.

The seeds of at least two other species of *Micrandra* are eaten in the northwest Amazon, but they seem to be used much less frequently than *M. Spruceana*. Along the Papuri River, in Colombia and Brazil, the Tukanos sometimes gather the seed of *Micrandra Sprucei* which are strewn abundantly on the floor of the sandy caatinga forest where this species is so common. *Micrandra Sprucei* perhaps has more oil in its seeds than has *M. Spruceana*. Its Tukano name *wa-só-ně-ně* means "light-rubber" ("wa-so" = *Hevea* and "ně-ně" = light), probably in reference to the use of the oil boiled from the seeds to light lamps. On the Piraparaná River, the seeds of *Micrandra Rossiana* are used as food. In all of these species, the process of boiling the seeds several times to remove the poisons and oils is identical.

It will be of interest to point out that the seeds of *Micrandra glabra* have been reported (8) as "edible" in British Guiana.

Large and fleshy, the seeds of *Vaupesia cataractarum* are a favourite food of the Desano Indians along the Vaupes River between Mitu and Javarete. The extraordinarily abundant harvest each year attracts bands of Indians, and huge canoe-loads of seeds are taken back to malocas in the neighbourhood. So far as I could learn, the method of preparing these seeds is the same as for *Micrandra*. The great profusion of seeds and the ease of gathering them on the high, well-drained slopes near rapids account for the natives' predilection for *Vaupesia* over all species of *Micrandra* and *Hevea*.

What has been outlined above would seem to show rather positively that any postulations resting on the supposition that the Indians choose only one or two species of *Hevea* as a food-source are without foundation in fact.

We must next turn our thoughts towards a consideration of the claims of cultivation or "domestication" of *Hevea* as a wild nut tree. What are the facts in this regard?

Both Seibert and Baldwin base their principal postulation on the fact that along the Rio Negro, where they feel that *Hevea* shows especial variability, the Indians eat rubber seeds. Seibert further allows himself to suggest that it was a custom "within the Amazon Valley itself" for "many an Indian to transplant seedlings from jungle to dooryard." This custom I have never seen amongst Indians. Indeed, I have never seen a *Hevea* tree growing—either planted or as a survival from felling—in the garden of the house of any primitive Indian anywhere in the Amazon Valley, including the northwestern part.

Here, we must distinguish between the primitive aborigine and the civilised rubber tapper (be he pure Indian, white or half-breed), who, in felling a few square feet of virgin jungle for his temporary shack, where he lives in the dry season only whilst tapping rubber, will almost never sacri-

fice a wild *Hevea* tree. The tappers' little palm-thatch huts and their clearings often will be lorded over by two or three majestic rubber trees that have been spared, in part because they are tapped on the tapper's regular daily rounds and in part for sentimental reasons ("the goose that lays the golden egg"). There is no such custom as planting in these little jungle plots. Nor are the tappers interested in the seeds as a source of food, partly because it is only the uncivilised Indian apparently who will eat them and partly because the seeds fall at the time of high water, when the tapper and his family never use the hut, which is under water, but have moved back to a town to their permanent home.

Even were we to vouchsafe that the tappers planted seedlings or spared trees near their temporary jungle dwellings, it would be irrelevant, insofar as any appreciable effect which these isolated trees may have had on the evolutionary course of the genus. For, prior to a century ago, there was no widespread use of rubber and, consequently, no tapping industry had as yet grown up which brought thousands of workers into intimate association with wild rubber trees. Even if the isolated trees spared by the lonely tapper near his hut had had the extreme effect through hybridisation with other trees of the vicinity, which Seibert and Baldwin propose and Anderson and Dijkman accept, the effects would not yet — in only one hundred years — be seen on the large scale and over the vast area that have been suggested. Nor can such casual cultivation be termed "domestication."

That Anderson considers the effects to have been appreciable over a wide area for hundreds of years is evident when he says (1):

When man gradually learned that the latex of *Hevea* also had its applications, he already had at hand variable, introgressed, semi-domesticated populations, in which trees superior in latex were more likely to be found. The extent and frequency of introgression must certainly vary greatly with the type of agriculture that is being practiced. Under the jungle-clearing pattern, like that just described for *Hevea*, it must have been at a maximum.

And further evidence of Anderson's lack of knowledge of Indian life in the northwest Amazon is shown by his statements that primitive man, having domesticated the rubber tree for its seeds, "brought into their small and transient villages" for planting trees selected for "superior nuts or a superior yield of nuts." This implies that the Indian selected for seeds, which, of course, with his very rudimentary agriculture, he would never have done, even had he planted the rubber trees.

Anderson refers to "supposedly wild trees" which he pictures as populating sites "now part of the jungle, but which indicate clearly that they had been village clearings before they were engulfed by the rapidly regenerating tropical brush." The truth of the matter is that the climatic climax of the northwest Amazon, as in other tropical rain-forests, is extraordinarily slow at taking over cleared areas, through numerous secondary successions. Literally centuries pass before the virgin or primary forest asserts itself, and one need not be a botanist to point out a patch where human dwelling

once disrupted the natural cover. This is so well known (23) that it need not here be discussed in any detail.

Anderson's statement that the "supposedly wild trees" of secondary communities supplied "some of our most potentially valuable breeding material" for high yield of latex is not borne out by the record of selection of élite jungle trees which botanist-explorers of the United States Department of Agriculture carried out in the Amazon Valley during the past ten or twelve years. Almost all of the most promising selections made by these botanists in Brazil, Colombia and Peru were of individuals growing in primary forest. In my own work of selection, for example, I was wont to avoid trees not in the climatic climax forest because of possible external influences on yield of latex which unnatural conditions in successive forests may have had.

It is true that, here and there along the Rio Negro and lower Uaupés in Brazil, groups of rubber trees — representing usually *Hevea guianensis* and *H. pauciflora* — grow near habitations or at abandoned house-sites under conditions that suggest that they might have been planted. I have seen such sites, and I have not the slightest doubt that they were planted. But this cultivation, it is of the most extreme interest to point out, is recent, dating no earlier than the beginnings of the rubber boom in the middle of the last century. And, in all cases, they are found at the sites inhabited by *caboclos* or half-breeds, never at settlements of uncivilised Indians. These people, though they are not of pure Indian blood and are civilised, may use *Hevea* seeds as a food, *but only when famine threatens*, not with the regularity and in the near-ceremonial way of the primitive Indian. And it must be emphasized here that the sites where one finds rubber trees under conditions suggestive of cultivation are not many. Surely, this "cultivation" would have to have been far more widespread and common to have had anywhere near the influence through hybridisation and introgressive hybridisation which Anderson and Dijkman present as established history.

If we continue our critical examination, we find that it is doubtful in the extreme that the *Hevea* trees which we see growing near houses along the Rio Negro were planted deliberately as a source of food. They may have been set out or spared in felling merely because they were "seringueiras" (rubber trees), even though neither of these two species is the one that is widely tapped for rubber along the Rio Negro. There is, nonetheless, an innate aversion to destroying any sort of rubber tree. And we must likewise consider the possibility that, as in the case of several other trees which yield no economic product, the rubber trees were set out merely as curiosities or ornamentals. Be that as it may, the unadorned facts about cultivation are these: (a) primitive Indians have not cultivated and do not now cultivate or care for rubber in any special way in their farms; (b) what little cultivation there is has been done by civilised inhabitants engaged directly or indirectly in rubber tapping; and (c) such cultivation on the Rio Negro is of relatively recent incipience and is extremely limited and localised.

A moment's thought will elucidate some of the reasons why the Indian never cultivates rubber and *cunuri* trees as a source of food.

Before the days of their reduction to civilisation, the Indians probably gathered *Hevea* and *Micrandra* seed as they do to-day: from wild trees. Many are the wild trees in the jungle that are visited every year in their fruiting time by Indians who often journey for several days to gather the nuts. I have seen this repeatedly in the Colombian Amazonia. No Indian relies upon rubber or *cunuri* trees planted or left standing in the yuca and coca fields around his house. All, without exception, garner their supply from the forest. When one lives long enough with these people, one realises the obvious and logical reason for this custom: the Indian enjoys such a harvesting trip through the jungle. It is a harvest that takes place but once a year, and it has, through the ages, come to be rather a ceremony or a kind of hunting task much to the Indian's liking. It is man's sport, whereas agriculture is left to the women. He would never think of giving up this enjoyment for the dullness of picking up the seeds near his house.

An Indian will live but a few years at one site. When he fells a patch for a house-site, the soil is leached out in a few years, and the leaf-cutting ant usually has multiplied to such an extent that it is a physical impossibility to continue to inhabit the site. Why, then, should he plant a tree that will not bear fruit in any appreciable amount under fifteen or more years, especially when the woods around his house or within easy journey are full of rubber trees? The answer is, of course, that he does not plant it at all. He might leave an occasional tree standing when he fells, but, as pointed out above, I have yet to see a rubber tree spared in the vicinity of a primitive Indian's dwelling.

Still another — and perhaps the most important — reason for not planting *Hevea* is fear of falling trees near dwelling places. None of the Indians of the northwest Amazon allows isolated trees to remain anywhere near the sites chosen for house-raising. The forest is felled clean: not one tree of any size is left standing and none is planted. Wind-storms in the Amazon are not infrequent and the sturdiest-looking trunk might easily be hollowed by rot and termite and an easy prey to the first strong blow. About the tallest tree that one sees near Indian habitations is the palm, *Guilielma speciosa*, but, as this medium-sized fruit-tree is rarely, if ever, victim of rot and, as its crown is light, it does not present the danger of falling that so often attends dicotyledonary trees of the forest.

The all-important theme in the postulations presented by Baldwin, Seibert, Anderson and Dijkman is that cultivation for edible seeds created optimum conditions for introgressive hybridisation. They give introgressive hybridisation supreme importance in *Hevea* evolution. It is not my purpose in this paper to discuss the role which this process may or may not have had, except to say that I hold that *Hevea* is probably no more variable than many other genera of tropical trees and that introgressive hybridisation has not had anywhere near the importance which is claimed for it. It is a temptation to overwork new approaches such as this, and especially so when "evidence" can be elaborated to present a

plausible series of arguments. I need not consider introgressive hybridisation here in detail simply because, as the summary and conclusion below bring out, the conditions which are stated to encourage wide-scale crossing and back-crossing to native species of *Hevea* do not exist and never did.⁴

Even though it be quite clear that extensive hybridisation of species of *Hevea* has not come to pass as a result of "domestication" of the rubber



FIGURE 2. Communal Makuna Indian house or *maloca*, Río Popeyacá, Colombia. Even though, in some tribes, the forest is close to houses, isolated forest trees are rarely, if ever, left standing near dwellings. Amongst most Indians of eastern Colombia, enormous clearings are made in the centre of which the house is built; in this case, too, all trees of any size are felled. The palm which is planted near the dwelling is *Guilielma speciosa*.

⁴ Since the preparation of this paper, I have had the opportunity of reading an extremely interesting article by J. G. Bouychou of the Institut Français du Caoutchouc in Paris ("Note sur l'amélioration de l'*Hevea*" ms. (1955)). Bouychou has postulated, as a partial basis for his proposed program of *Hevea* improvement, that the wild rubber trees in the Amazonian forest are highly inbred. This has resulted, according to Bouychou, from the wide isolation of the individual trees. The discovery that midges are the chief, if not the only, natural pollinators of *Hevea* and that *Hevea* pollen normally is not shed as far as the usual distance between individual trees in the forest are offered as support of this postulation. Without entering into a thorough examination of Bouychou's novel point of view, I may say here that many field observations which I have made in the forest as well as some of the results of recent selection and breeding work would seem to support the hypothesis which, of course, is diametrically the opposite of that proposed by Baldwin and Seibert.

tree for food, we still must grant that natural hybridisation probably has had some part in the evolution of the genus. We know that there are no barriers to hybridisation between the species, all of which have been crossed artificially.

In areas where man has caused great upheaval in the natural vegetation, we have undoubted proof of crossing. This is true of such places as the outskirts of the towns of Manáos and Iquitos (13, 37, 40). Specimens collected in such localities exhibit extremes of variation and all possible intergrades, some of which have erroneously been described, in the past, as varieties or forms. Trees left standing alone in extensively cleared areas are disrupted in their flowering rhythm and blossom almost all year through. This, together with their proximity with no interfering forest canopy, permits different species to cross freely. But even this clearing, extensive as it is in several localities, has happened only in recent times and can have had no appreciable effect on generic evolution.

Conditions are very different in the forest. Sometimes — though not so frequently as often supposed — two or more species grow together. I have noticed in the Amazon, however, that each species seems to have its own flowering time. To be sure, all species of *Hevea* flower at the beginning of the dry season, but all do not blossom in strict simultaneity. Pistillate flowers in *Hevea* are known to have a relatively short period of receptiveness (three or four days in *H. brasiliensis* (17)). There is enough disjunctiveness in flowering times to prevent appreciable natural hybridisation. That there is really little crossing in nature is borne out by long study of trees in the field and by close examination of herbarium specimens, both of which indicate that *Hevea* is not excessively variable.

This may seem to be at sharp variance with those who see every variation as evidence of "penetration" of genes from alien species. It is not, however, at variance with what I have found in the field, and Ducke (15), after more extensive field work on the genus than any living botanist, concurs. Consequently, I am forced to differ most vehemently with those who consider that in wild *Hevea* "introgression . . . is readily perceptible and of great biological import . . ." and that "one can find its influence . . . for all the species" (6).

SUMMARY

1. The Indians of the northwest Amazon utilise the seeds of a number of species of *Hevea*, *Micrandra* and *Vaupesia* regularly each year and sometimes ceremonially as a food.

2. Recent hypotheses have postulated that a) because of their interest in *Hevea* as a food-plant, the Indians cultivated trees which were selected for superior nuts or yield of nuts; b) species were carried by Indians for planting to areas far beyond their natural range; c) trees of very different provenience were planted together; d) these cultivations were later abandoned to the jungle; e) the plantings greatly enhanced the opportunities for hybridisation, and the hybrid offspring in turn crossed back to the

native, local species; f) this led to "mongrel swarms" with the excessive "variability characteristic of mongrels."

3. An exposition of the facts as found through long field work in the northwest Amazon does not support these hypotheses because a) the Indian uses seeds from wild trees and never cultivates them; b) trees occur near a few house-sites under conditions which might possibly be cultivation, but these were not planted out by the primitive Indian who eats seeds and are of such recent cultivation that they could not have had any appreciable effect on the evolution of the genus; c) due to its very short-lived seeds, *Hevea* could not be carried about by Indians over wide areas on their migrations.

CONCLUSION

It would appear that, contrary to previous suggestions, the claims as to the effect of cultivation and "domestication" of rubber resulting from its use as a food, while plausible on the surface, are unwarrantably sweeping and their soundness suspect. It is altogether probable that man has had little, if any, appreciable influence on the overall course of evolution in the genus *Hevea*.

LITERATURE CITED

1. ANDERSON, EDGAR. "Introgressive hybridization" 78. 1949.
2. ———. "Plants, man and life" 130. 1952.
3. AUBLET, FUSÉE. "Histoire des plantes de la Guayane Française" 2: 871. 1775.
4. BALDWIN, J[OHN] T., JR. "Hevea: a first interpretation" in Journ. Hered. 38: 54. 1947.
5. ———. "Hevea rigidifolia" in Am. Journ. Bot. 34: 261. 1947.
6. ———. "Introgressive hybridization" in Journ. Hered. 40: 256. 1949.
7. ———. "Loss of oil from Hevea seed" in Journ. Hered. 40: 47. 1949.
8. ——— and RICHARD EVANS SCHULTES. "A conspectus of the genus *Cunuria*" in Bot. Mus. Leaflet. Harvard Univ. 12: 325. 1947.
9. BENTHAM, GEORGE. "On the north Brazilian Euphorbiaceae in the collections of Mr. Spruce" in Hooker, Journ. Bot. 6: 368. 1854.
10. DIJKMAN, M. J. "Hevea — Thirty years of research in the Far East" 256. 1951.
11. DUCKE, ADOLPHO. "Revision of the genus *Hevea*, mainly the Brazilian species" in Arch. Inst. Biol., Veg. Rio Janeiro 2: 217. 1935. [Reprinted in 1939 and in Portuguese, 1941].
12. ———. "A flora do Curicuriari, afluente do Rio Negro . . ." in An. Prim. Reun. Sul-Am. Bot. 3: 396. 1938.
13. ———. "Novas contribuições para o conhecimento das seringuerias (*Hevea*) da Amazônia Brasileira" in Agr. Serv. Florest. Rio Janeiro 2: 25. 1943.
14. ———. "Novas contribuições para o conhecimento das seringuerias da Amazônia Brasileira." II. in Bol. Técn. Inst. Agron. Norte no. 10: 1946.
15. DUCKE, A[DOLFO]. "Critical notes on some Amazonian plants" in Bol. Técn. Inst. Agron. Norte no. 19: 46. 1950.

16. ——— AND GEORGE A. BLACK. "Phytogeographical notes on the Brazilian Amazon" in *Anais Acad. Bras. Cienc.* **25**(1): 1. 1953.
17. HEUSSER, C. "Over de Voortplantingsorganen van *Hevea brasiliensis* Müll.-Arg." *Rubber Ser. Bull. Gen. Exp. Sta. A.V.R.O.S.* no. **24**: 1919.
18. HUBER, J[ACQUES]. "Ensaio d'uma synopse das especies do genero *Hevea* sob os pontos de vista systematico e geográfico" in *Bol. Mus. Para.* **4**: 620. 1906.
19. LARUE, CARL D. "The *Hevea* rubber tree in the Amazon Valley" *U. S. Dept. Agric., Dept. Bull.* no. **1422**: 1926.
20. LECOINTE, PAUL. "A Amazônia Brasileira" **3**: 145. 1934.
21. PAX, F. in Engler: *Pflanzenreich IV*, **147**: 117. 1910.
22. RANDS, R. D. AND LOREN G. POLHAMUS. "Progress report on the cooperative *Hevea* rubber development in Latin America" *U.S.D.A. Circ. No.* **976**: 1955.
23. RICHARDS, P[AUL] W. "The tropical rain forest" 264, 265, 377-403. 1952.
24. SCHULTES, RICHARD EVANS. "The genus *Hevea* in Colombia" *Bot. Mus. Leaf. Harvard Univ.* **12**: 1. 1945.
25. ———. "Plantae Colombianae X" in *Caldasia* **3**: 247. 1945.
26. ———. "Glimpses of the little known Apaporis River in Colombia" in *Chron. Bot.* **9**: 123. 1945.
27. ———. "Aprovechamiento científico de una riqueza natural colombiana" in *Agr. Trop.* **1**(12): 31. 1946.
28. ———. "Estudio preliminar del género *Hevea* en Colombia" in *Rev. Acad. Col. Ciénc. Exact. Físico-Quím. Nat.* **6**: 331. 1945; in *Rev. Fac. Nac. Agron.* **6**: 18. 1946.
29. ———. "Studies in the genus *Hevea* I" *Bot. Mus. Leaf. Harvard Univ.* **13**: 1. 1947.
30. ———. "Studies in the genus *Hevea* II" *Bot. Mus. Leaf. Harvard Univ.* **13**: 97. 1948.
31. ———. "The importance of plant classification in *Hevea*" in *Econ. Bot.* **3**: 84. 1949.
32. ———. "La importancia de la taxonomía en el estudio de los cauchos *Hevea*" in *Trop. Agric.* **7**: 33. 1951.
33. ———. "La importancia de la taxonomía en el género *Hevea*" in *Lilloa* **18**: 287. 1949.
34. ———. "El cauchero abanderado del Vaupés" in *El Financ.* no. **8**: 39. 1952; in *Rev. Nac. Agr.* no. **564**: 1. 1952.
35. ———. "Studies in the genus *Hevea* IV" *Bot. Mus. Leaf. Harvard Univ.* **15**: 111. 1952.
36. ———. "Studies in the genus *Micrandra* I" *Bot. Mus. Leaf. Harvard Univ.* **15**: 201. 1952.
37. ———. "Studies in the genus *Hevea* VI" *Bot. Mus. Leaf. Harvard Univ.* **15**: 255. 1952.
38. ———. "Una reseña fitogeográfica de la Amazonía noroeste" in *Amaz. Col. Amer.* **4**: 195. 1953; *Trop. Agr.* **9**: 1953.
39. ———. "A new generic concept in the Euphorbiaceae" in *Bot. Mus. Leaf. Harvard Univ.* **17**: 27, *tt. 12, 14*. 1955.
40. SEIBERT, R[USSELL] J. "A study of *Hevea* (with its economic aspects) in the Republic of Peru" in *Ann. Mo. Bot. Gard.* **34**: 261. 1947.
41. ———. "The uses of *Hevea* for food in relation to its domestication" in *Ann. Mo. Bot. Gard.* **35**: 117. 1948.

EXPLANATION OF PLATES

PLATE I. *Hevea Benthamiana* Muell.-Arg. 1) Flowering branch, about $\frac{1}{2}$ natural size; 2) Fruiting branch, about $\frac{1}{2}$ natural size; 3 and 4) Leaf variations, about $\frac{1}{2}$ natural size; 5) Valve of capsule, about $\frac{1}{2}$ natural size; 6) Seeds, about $\frac{1}{2}$ natural size; 7) Pistillate bud, about $5 \times$ natural size; 8) Pistillate flower, about $5 \times$ natural size; 9) Ovary with calyx removed, about $7\frac{1}{2} \times$ natural size; 10) Staminate bud, about $5 \times$ natural size; 11) Staminate flower, about $5 \times$ natural size; 12) Staminal column with calyx removed, about $7\frac{1}{2} \times$ natural size; 13) Section of under surface of leaf, about $7\frac{1}{2} \times$ natural size.

PLATE II. *Hevea nitida* Muell.-Arg. 1) Flowering branch with young leaves, about $\frac{1}{2}$ natural size; 2) Fruiting branch, about $\frac{1}{2}$ natural size; 3) Leaf variations, about $\frac{1}{2}$ natural size; 4) Valve of capsule, about $\frac{1}{2}$ natural size; 5) Seeds, about $\frac{1}{2}$ natural size; 6) Staminate bud, about $5 \times$ natural size; 7) Staminate flower, about $5 \times$ natural size; 8) Staminal column with calyx removed, about $7\frac{1}{2} \times$ natural size; 9) Pistillate flower, about $5 \times$ natural size; 10) Pistillate bud, about $5 \times$ natural size; 11) Ovary with calyx removed, about $7\frac{1}{2} \times$ natural size.

PLATE III. *Hevea nitida* Muell.-Arg. var. *toxicodendroides* (Schult. & Vinton) R. E. Schultes. 1) Flowering branch, about $\frac{1}{2}$ natural size; 2) Fruiting branch, about $\frac{1}{2}$ natural size; 3 and 4) Leaf variations, about $\frac{1}{2}$ natural size; 5) Valve of capsule and seeds, about $\frac{1}{2}$ natural size; 6) Staminate bud, about $5 \times$ natural size; 7) Staminate flower, about $5 \times$ natural size; 8) Staminal column with calyx removed, about $7\frac{1}{2} \times$ natural size; 9) Pistillate flower with one calyx lobe removed, about $5 \times$ natural size; 10) Pistillate bud, about $5 \times$ natural size; 11) Ovary with calyx removed, about $7\frac{1}{2} \times$ natural size.

PLATE IV. *Hevea rigidifolia* (Spruce ex Benth.) Muell.-Arg. 1) Flowering branch, about $\frac{1}{2}$ natural size; 2) Leaf variations, about $\frac{1}{2}$ natural size; 3) Valve of capsule, about $\frac{1}{2}$ natural size; 4 and 5) Seed, about $\frac{1}{2}$ natural size; 6) Pistillate bud, about $5 \times$ natural size; 7) Pistillate flower, about $5 \times$ natural size; 8) Ovary with calyx removed, about $7\frac{1}{2} \times$ natural size; 9) Staminate bud, about $5 \times$ natural size; 10) Staminate flower, about $5 \times$ natural size; 11) Staminal column with calyx removed, about $7\frac{1}{2} \times$ natural size.



HEVEA BENTHAMIANA Muell.-Arg.



HEVEA NITIDA Muell.-Arg.



HEVEA *nitida* Muell.-Arg.
var. *toxicodendroides*
(Schult. & Vinton) R.E.Schult.

HEVEA NITIDA Muell.-Arg. var. TOXICODENDROIDES (Schult. & Vinton) Schultes



HEVEA RIGIDIFOLIA (Spruce ex Benth.) Muell.-Arg.

STUDIES IN THE THEACEAE, XXVIII
MELCHIORA, A NEW GENUS IN AFRICA

CLARENCE E. KOBUSKI

APPROXIMATELY ten years ago while reviewing the genus *Adinandra*¹ I was both impressed and intrigued by the presence of two unusual species quite isolated in Africa and far removed from the Asiatic-Malaysian taxa of the genus. Furthermore, these two African species were two thousand miles distant from each other. One, *Adinandra mannii* Baker, obviously a very rare species, has been found only on the tiny island of St. Thomas, close to but off the western coast of Africa in the Gulf of Guinea. The second species, *A. schliebenii* Melchior, was described from material collected near the eastern coast of Africa in the Territory of Tanganyika, separated from the first species by the span of the complete continent. In 1950, three years after my paper on *Adinandra* had been published, a third species *A. intermedia* Boutique & Troupin was described from Belgian Congo, Uganda and the Territory of Tanganyika. While having many fundamental characteristics of the genus *Adinandra* these three taxa have several distinct features which clearly set them apart.

Szyszyłowicz (1893) in his treatment of the family for *Die Natürliche Pflanzenfamilien* recognized in the one African species (*A. mannii*) described at that time enough differences to establish a new section *Eleutherandra* based primarily on the free stamens in the flower. Two other sections were introduced at the same time. The three sections were as follows:

Sect. I. ELEUTHERANDRA: Stamens free

Sect. II. EUADINANDRA: Stamens in bundles

Sect. III. SYMPHIANDRA: Stamens joined and disposed in a tube

Later, in 1925, Melchior continued the use of these sections but added a fourth, *Eleutherostyla*, separating his new section from those of Szyszyłowicz on the basis of the free styles. This last section of Melchior is now the New Guinea genus *Archboldiodendron*. At the time of his treatment Melchior stated that the knowledge of the stamens was too incomplete to group the species by sections, especially in Sections II and III, which comprise the Asian-Malaysian species and as a result treated all the species geographically. I found it expedient to follow Melchior's method of treatment for two reasons. In the first place, except for the taxa *A. millettii* (China) and *A. dumosa* (Malaysia) the species are endemics of very limited range. Secondly, eight out of every ten specimens of *Adinandra* have been collected in the fruiting stage and many taxa have been described from the fruit alone. Furthermore, it is difficult, in working with

¹ Studies in the Theaceae, XV. A review of the genus *Adinandra*. Jour. Arnold Arb. 28: 1-98. 1947.

herbarium material, to place a species definitely in its respective section even with the stamens present.

The second species of the African section *Eleutherandra*, *A. schliebenii*, was described by Melchior in 1934. In this treatment Melchior gave a very interesting and enlightening discussion of the species, quoting excerpts from a letter written by the collector, H. J. Schlieben and contrasting the new taxon with *A. mannii* described sixty-six years earlier.

Besides the free stamens used as a means of separating these three species from the other taxa in *Adinandra* there are other features of importance which set them apart and which taken together form a group worthy of generic distinction.

The features of distinction are as follows: (1) Stamens few, in a single series, the filaments glabrous and free except at the very base, the anthers glabrous (without setae) and subsagittate; (2) Corolla-lobes orange and red, three times longer (35–50 mm.) than the calyx-lobes, connate at the base only, otherwise free, disposed in a pseudo-tube, the apices of the lobes arching over the pistil and stamens.

The feature of relationship with *Adinandra* is found in the fruit. The indehiscent capsules are 4-celled, incompletely 5-celled or 5-celled, with many small, reniform, shiny seeds. The placentae are bifid.

It is a pleasure to name this new genus *Melchiora* for Professor Hans Melchior of the Botanisches Museum at Berlin-Dahlem, Germany. For years Professor Melchior has shown a continued interest in and has made many valuable contributions to our knowledge of the family Theaceae. The section name *Eleutherandra* is not available for generic use since it has been used by Van Slooten (1925) for a genus in the Flacourtiaceae. Another name, *Adinandropsis* has been published as a *nomen nudum*.

Melchiora, gen. nov.

Adinandropsis Pitt-Schenkel in Jour. Ecol. 26: 80. 1938, nom. nud.

Arbores. Folia alternata, simplicia, chartacea vel subcoriacea, penninervia. Flores hermaphroditi, in axillis foliorum solitarii; bracteolae duae, persistentes; sepala quinque, imbricata, concava, persistentia, crassa inaequalia, exteriora satis breviora; petala quinque, libera; stamina uniseriata, pauca (15–35), filamentis filiformibus, glabris, liberis (inter se), basi ad corollam adnatis, antheris glabris (sine setis), basi cordato-sagittatis, apice apiculatis; ovarium quattorloculare, vel quinqueloculare, multiovulatum, placenta in quoque loculo bifida, stylo filiformi, stigma leviter quinqsulcatum. Fructus indehiscens, in sicco subligneus, sepalis bracteolisque persistentibus. Semina in quoque loculo multa, parva, reniformia, testa brunnea, nitida, reticulata.

TYPE SPECIES: *M. mannii* (*Adinandra mannii* Baker).

KEY TO THE SPECIES

Young branchlets tuberculate-punctate; leaves subrotund at the base; ovary 4-celled, glabrous; style glabrous. *M. mannii*.

Young branchlets smooth; leaves cuneate at the base; ovary 5-celled, sericeous; style sericeous on lower portion, glabrous upper part.

Petals acute and entire at the apex; the inner three sepals sericeous on the dorsal surface, the outer two glabrous; stamens 15–20. *M. schliebenii*.

Petals obtuse or rounded and denticulate at the apex; all sepals glabrous without, sericeous within; stamens 25–35. *M. intermedia*.

Melchiora mannii (Oliver), comb. nov.

Adinandra mannii Oliver in Fl. Trop. Afr. 1: 170. 1868. — Hooker, Icon. Pl. 11: 29, t. 1039. 1867. — Szyszyłowicz in Nat. Pflanzenfam. III. 6: 189. 1893. — Melchior in Notizbl. Bot. Gart. Mus. Berlin 8: 657. 1924; 11: 1100. 1934; in Nat. Pflanzenfam. ed. 2, 21: 144. 1925. — Exell, Cat. Vasc. Plts. S. Tomé 112. 1944. — Kobuski in Jour. Arnold Arb. 28: 94. 1947. — Boutique & Troupin in Bull. Jard. Bot. Bruxelles, 20: 65. 1950.

DISTRIBUTION: West Africa (Island of St. Thomas).

ISLAND OF ST. THOMAS: summit of the peak on the island, *G. Mann 1066* (ISOTYPE, GH).

Tree 10 m. high; branches gray, terete, glabrous, the young branchlets red-brown, glabrous, terete, minutely tuberculate-punctate, the terminal buds glabrous. Leaves chartaceous to subcoriaceous, oblong-elliptic to oblong-obovate, quite uniform in size, 6–7 (–9) cm. long, 2–3 cm. wide, acuminate at the apex, asymmetrical, subrotund at the base, glabrous on both surfaces, the midrib reddish near the base, tuberculate-punctate on the lower surface, the margin glandular-denticulate, the veins 15–18 pairs, conspicuous but not prominent, anastomosing midway to the margin, the petiole 1–2 mm. long. Flowers axillary, ? solitary; pedicel ca. 2 cm. long (fide Oliver), glabrous; bracteoles 2, persistent, glabrous, opposite, immediately below the calyx, broadly ovate, 7–8 mm. long, 5–6 mm. wide, acute at the apex, carinate; calyx-lobes 5, imbricate, glabrous on the exterior surface, very lightly appressed-pubescent (with binocular) on the interior surface, broadly ovate, acute at the apex, unequal, the two outer lobes 12–14 mm. long, ca. 10 mm. wide, the three inner lobes 17–19 mm. long, ca. 10 mm. wide, their inner margins scarious, entire; corolla-lobes 5, slightly connate only at the very base, not spreading, somewhat tubuliform, oblong, ca. 25 (35–45) mm. long, 7–10 mm. wide, obtuse to subrotund at the apex; stamens ca. 30 in a single series, equal, ca. 10 mm. long, the filaments glabrous, ca. 6 mm. long, adnate to the base of the corolla, otherwise free, the anthers oblong-linear, ca. 4 mm. long, strictly glabrous, the apicule less than 0.5 mm. long, truncate to emarginate; ovary conical-ovoid, glabrous, ca. 4 mm. diam., tapering into the style, 4-celled, multi-ovulate, the placentae bifid, the style glabrous, entire, ca. 22 mm. long, the stigma 4-lobed. Fruit not seen.

An examination of the isotype in this species shows that the ovary is distinctly 4-celled. A 4-celled ovary is unusual in the Theaceae. However, in *Adinandra* two species, *A. myrioneura*, of British North Borneo, and

A. oblonga, of Siam, have 4-celled ovaries with innumerable small ovules, like that found in this species.

One might expect, from an examination of more material of the species, to find specimens in which the ovary is 5-celled as in *M. intermedia*. According to Exell, however, the species may be no longer in existence. In his Catalogue of the Vascular Plants of S. Tomé (p. 113. 1944) he states: "I made a hasty search for *A. Mannii* on the Pico in November 1932, but without success. A tremendous rainstorm was in progress and one could see only a few yards. The vegetation near the summit of the Pico has been partially cleared and some *Cinchona* planted, so that it is possible that *A. Mannii* is now extinct. It was last collected by Campos in 1907."

There are other isolated species in the Theaceae that have suffered a like fate. *Freziera cordata* Tulasne, known only from Martinique, was obliterated in the devastating volcanic eruption of Mt. Pelée on that island in 1902. *Franklinia alatamaha* Marshall, found only in Georgia near Fort Barrington in McIntosh County, was last collected in the late eighteenth century. This species was probably exterminated as a spontaneous plant in the years 1787 and 1789 by nurserymen in an effort to fill large orders for the species for a London firm.

***Melchiora schliebenii* (Melchior), comb. nov.**

Adinandra schliebenii Melchior in Notizbl. Bot. Gart. Mus. Berlin 11: 1076, 1097. 1934. — Kobuski in Jour. Arnold Arb. 28: 95. 1947. — Boutique & Troupin in Bull. Jard. Bot. Bruxelles, 20: 65. 1950.

DISTRIBUTION: East Africa (Tanganyika Territory).

TANGANYIKA TERRITORY: Uluguru, in fog forest northwest side of Lupanga Mountains; tree 20–30 m., flowering and fruiting, with orange and red flowers, *H. J. Schlieben* 3175, (ISOTYPE, AA), December 28, 1932.

Tree 20–30 m. high; very young branchlets smooth, compressed, glabrous, red to gray-brown. Leaves chartaceous to coriaceous, obovate-oblong, 5–10 cm. long, 2–3.5 cm. wide, acute at the apex or shortly and obtusely acuminate, cuneate at the base, glabrous on both surfaces, the midrib red beneath, the margin serrulate-dentate, glandular, the veins conspicuous beneath because of the red color, the petiole ca. 5 mm. long. Flowers axillary, solitary, ca. 3 cm. long; pedicels 2.5–3.5 cm. long, recurved, glabrous; bracteoles 2, persistent, opposite, immediately below the calyx, glabrous, broadly ovate, acute at the apex, carinate, the outer one 3 mm. long and wide, the inner one 5 mm. long and wide; calyx-lobes 5, imbricate, ovate, acute at the apex, unequal, varying in length from 10 mm. (outer lobe) to 17 mm. (inner lobe), ca. 12 mm. wide, the two outer lobes glabrous on the exterior surface, the three inner lobes sericeous on the exterior surface except along the scarious margins, ciliolate; corolla-lobes 5, free, twice as long as the innermost calyx-lobe, linear-oblong, 32–45 mm. long, 5–7 mm. wide, acute at the apex, somewhat narrowed and connate at the base, not spreading, somewhat tubuliform; stamens 15–20, uni-

seriate, ca. 15 mm. long, glabrous, the filaments free (inter se), adnate to the base of the corolla, filiform, 8–9 mm. long, the anthers linear, ca. 5 mm. long, cordate-sagittate at the base, the connective projected at the apex into a small subulate-lanceolate apicule 1 mm. long; ovary conical, ca. 6 mm. long, 4 mm. diam., sericeous-tomentose, imperfectly 5-celled, multi-ovulate, attenuate at the apex into a filiform style 24–30 mm. long, sericeous along the lower portion, glabrous along the upper portion, lightly 5-sulcate, the stigma minute, lightly 5-sulcate. Fruit indehiscent, conical-ovoid, ca. 2 cm. long, 1 cm. diam., the seeds many, small, reniform, 1.2–1.5 mm. diam., brown, shiny, reticulate.

Whereas *Melchiora mannii* has been shown to have been a rare species of very limited geographical range, *M. schliebenii* is known to enjoy a well-established stand in Tanganyika Territory. Quoting from a letter by the collector (H. J. Schlieben), Melchior records a stand of many trees and that the species seems to flower throughout the year. He mentions that on the east side of Magali Mountain (alt. 2450 m.), seventy percent of the trees are of this species. The trees are severely forked at this altitude. He also states that the heartwood is very hard and red in color.

There are other instances in the family Theaceae in which species are known to dominate isolated areas. On the tabletop mountains in Venezuela three species of *Bonnetia* are sufficiently abundant to form what are known as "Bonnetia forests." On Ptari-tepuí one finds *B. steyermarkii* forming impenetrable thickets and also mixed with *B. roraimae* in "Bonnetia roraimae forests." *Bonnetia sessilis* is the dominant species on the mesa between Ptari-tepuí and Sororopan-tepuí. All of these species, although abundant, are strict endemics.

***Melchiora intermedia* (Boutique & Troupin), comb. nov.**

Adinandra intermedia Boutique & Troupin in Bull. Jard. Bot. Bruxelles, 20: 62. 1950.

Adinandropsis, sp. nov. Pitt-Schenkel in Jour. Ecol. 26: 80. 1938, nom. nud.

DISTRIBUTION: Belgian Congo, Uganda, Tanganyika Territory. — Fide Boutique & Troupin.

NO SPECIMENS EXAMINED.

Trees erect, up to 40 m. high; branchlets glabrous, leaves generally disposed at the ends of the branchlets, chartaceous to submembranaceous, elliptic, oblong-elliptic or obovate, 7–13 (–18) cm. long, 2–4 (–6) cm. wide, acute or shortly acuminate at the apex, cuneate at the base, glabrous on both surfaces, green above, pale or yellow-green below, the midrib sulcate above, somewhat prominent beneath, the secondary nerves 17–20, red, the margin serrulate-dentate, the petiole ca. 5 mm. long. Flowers axillary, solitary, 3.5–5 cm. long; pedicel 1–3 cm. long, glabrous; bracteoles 2, persistent, unequal, suborbicular, often subacute at the apex, the outer one 2–4 mm. long and wide, the inner one 7–9 mm. long and wide; calyxlobes 5, imbricate, unequal, 1.5–3 cm. long, 1.2–1.6 cm. wide, the outer one

often subrotund at the apex, the others acute at the apex, glabrous externally, sericeous within; corolla-lobes 5, free, glabrous, erect, slightly connate at the base, somewhat tubular, 3.5–5 cm. long, 5–7 mm. wide, obtuse to rounded and denticulate at the apex; stamens 25–35, uniseriate, 11–16 mm. long, glabrous, the filaments free, filiform, 6–8 mm. long, lightly adnate to the base of the corolla, the anthers linear, cordate-sagittate, 5–8 mm. long, the connective projected at the apex into a small subulate-lanceolate apicule 0.7–1.5 mm. long; ovary conical, 5–10 mm. long, 3–6 mm. across, sericeous-tomentose, 5-celled, multi-ovulate, alternate at the apex into a filiform style 3–5 cm. long, sericeous along the lower portion, glabrous toward the apex, the stigma minute, lightly sulcate. Fruit indehiscent, conical-ovoid, 2–3 cm. long, ca. 1 cm. across, the seeds many, reniform or discoid, ca. 1 mm. diam., reticulate.

Unfortunately, none of the four specimens cited by Boutique & Troupin has been available for this study. However, in preparing an English description, I was impressed by the great similarity between *M. intermedia* and the earlier species, *M. schliebenii* described by Melchior.

The apex of the corolla-lobes is described as obtuse to rotundate and denticulate. As illustrated in the original publication, this denticulation appears very distinctive. Another character, the absence of pubescence on the external surface of the inner lobes of the calyx also distinguishes the species from *M. schliebenii*.

The other differences of importance appear to be those of size. I list below a comparison of these sizes as found in the two taxa *M. schliebenii* and *M. intermedia*. One will observe that there is greater variation listed for *M. intermedia* than for *M. schliebenii*. It is also obvious that in these two taxa the listed measurements are equal or overlap. Probably the reason is because Boutique & Troupin had four specimens from which to draw their conclusions while Melchior described his species from a single specimen.

	<i>M. schliebenii</i>	<i>M. intermedia</i>
HABIT:	Tree 20–30 m. high; severely forked	Trees to 40 m. high; erect
LEAVES:	5–10 cm. long; 2–3.5 cm. wide	7–13 cm. long; 2–4 cm. wide
PETIOLE:	5 mm. long	5 mm. long
PEDICEL:	2.5–3.5 cm. long	1–3 cm. long
BRACTEOLAS:	outer: 3 mm. long & wide inner: 5 mm. long & wide	outer: 2–4 mm. long & wide inner: 7–9 mm. long & wide
SEPALS:	10–17 mm. long, 12 mm. wide	15–30 mm. long, 12–16 mm. wide
PETALS:	32–45 mm. long, 5–7 mm. wide	35–50 mm. long, 5–7 mm. wide
FILAMENTS:	8–9 mm. long	6–8 mm. long
ANTHERS:	5 mm. long	5–8 mm. long
CONNECTIVE:	1 mm. long	1 mm. long
OVARY:	6 mm. long, 4 mm. diam.	5–10 mm. long, 3–6 mm. diam.
STYLE:	24–30 mm. long	30–50 mm. long

The distribution of *M. intermedia* as recorded by the authors appears to be far more extensive than that of the other two taxa. In fact, it almost invades the area recorded for *M. schliebenii*, since it has been recorded from Usambara (*Pitt-Schenkel* 376) in the Territory of Tanganyika, a locality only a little more than a hundred miles north along the coast from the type locality of *M. schliebenii*.

Another interesting comparison is that Schlieben, the collector of *M. schliebenii*, records his material as coming from an area in which the tree is the dominant element of the flora. Michelson, the collector of the type of *M. intermedia*, also records his specimen as coming from an area in which this species is the dominant element.

It seems that in the case of these two species, both dominating the flora of rather extensive localities which perhaps overlap, an opportunity to make a population study of the taxa in the woody family Theaceae may be afforded. This is indeed a rare opportunity, since the species in this family are usually isolated indigens and are seldom found growing abundantly or in close enough proximity to warrant such a study. Considering the great variation found within the taxa of this family, further study of ample material may show *M. schliebenii* and *M. intermedia* to constitute a single variable species.

A TAXONOMIC REVISION OF *PODOCARPUS*
X. THE SOUTH PACIFIC SPECIES OF SECTION *EUPODOCARPUS*,
SUBSECTION D

NETTA E. GRAY *

THE SPECIES AND VARIETIES of *Podocarpus* in subsection D of section *Eupodocarpus* are: *Podocarpus totara* D. Don, *P. hallii* Kirk, *P. nivalis* Hooker, *P. nivalis* var. *erectus* Cockayne, *P. acutifolius* Kirk, *P. alpinus* R. Brown, *P. gnidioides* Carrière and *P. nubigenus* Lindley. All of these are found in southern regions of the Pacific Ocean. Of the species growing in the southwest, all are found on the large islands: New Zealand, New Caledonia and Tasmania. *Podocarpus alpinus*, on Tasmania, is also found in the southeastern part of the continent of Australia. *Podocarpus nubigenus* is the only one of these species growing on the American side of the Pacific; it is found in the mountainous regions of southern Chile and, incidentally, has the southernmost range of any podocarp. Orr (15), using only geographical groups in the section *Eupodocarpus*, discussed *P. gnidioides* and *P. nubigenus* as exceptions in their areas. However, in his discussion of the New Zealand members, he emphasized the similar characteristics of all of them. The interesting distribution of these species, in the southern parts of South America and Australia and in New Zealand, is also found in other groups of plants and is considered when theories of land bridges or continental drift are under discussion (2).

Podocarpus totara, *P. hallii* and *P. nubigenus* are the only species with tree habit and large enough to be of some use in industry. *Podocarpus acutifolius* and *P. nivalis* var. *erectus* are erect but shrubby. *Podocarpus gnidioides*, *P. alpinus* and *P. nivalis* are low shrubs often having prostrate or decumbent branches. They are all small-leaved, exceeding 2 cm. in length only in *P. hallii* and *P. nubigenus* and exceeding 3.5 mm. in width also in *P. totara*. The small, crowded leaves, together with the low shrubby nature of several of the species, make the taxoid appearance of these plants quite apparent. The ridges on the twigs, formed by the decurrent petioles, are less prominent in *P. totara* and *P. hallii* and the leaves are not so densely crowded.

In the leaf anatomy one can see that these species belong in section *Eupodocarpus*. Some of the characters in common with other members of this section are a single midvein, stomata only on the lower surface, varying amounts of hypoderm on both sides and palisade mesophyll only on the upper side of the leaf.

* The author wishes to express her appreciation to Prof. A. Guillaumin of the Paris Museum Herbarium for permission to examine critical specimens. She wishes to acknowledge the assistance of the late Prof. John T. Buchholz in the interpretation of specimens from New Caledonia and the examination of those in the Paris Museum Herbarium. She thanks also Dr. H. W. Rickett of The New York Botanical Garden for special interpretation of the International Code of Botanical Nomenclature.

All of these species differ in their leaf anatomy from the rest of section *Eupodocarpus* by the absence of an organized accessory transfusion tissue. The lignified elements in the mesophyll, representing the accessory transfusion tissue, show variation both in the degree of lignification of single cells and in the number of cells in which the walls are so thickened. Juvenile and young leaves may not show any thickening of mesophyll cell walls, while mature leaves from exposed situations and from fruiting branches may have adjacent cells extending from the vascular transfusion tissue to the margin of the blade of the leaf. *Podocarpus gnidioides* shows these cells loosely arranged in a tissue (15, pl. 2, fig. 6) but they can scarcely be said to be oriented transversely to the blade of the leaf as in *P. totara*. Among these species, *P. gnidioides* has the most thickening and *P. acutifolius* the least. These lignified elements resemble those of section *Afrocarpus* rather than typical accessory transfusion tissue. Griffin (12) made a study of their development in *P. totara* and regarded them as belonging to true accessory transfusion tissue. However, Orr (15) speaks of this as a "misnomer" and considers them only as strengthening units similar to the lignified, pitted cells found in the mesophyll and palisade of section *Eupodocarpus* subsections A, B and C, rather than conducting elements even though here in subsection D they have not been found in either of the mentioned positions. Entertaining Orr's view, subsection D would not have accessory transfusion tissue. A dual role, conduction and support, is usually understood for lignified, pitted elements in vascular tissues. It hardly seems necessary in this case to ascribe one of these functions to auxiliary sclereids for all species to the complete exclusion of the other. Certainly even transversely oriented parenchyma cells also serve in conduction. These cells with thickened walls, regardless of number, often retain protoplasmic substances. The cells derive their origin from differentiating mesophyll whether they are true organized accessory transfusion tissue, isolated sclereids in the same location in the leaf, or auxiliary sclereids among or adjacent to the palisade tissue. This has very recently been observed by Griffith (13) while studying the ontogeny of vascular transfusion tissue in *Podocarpus macrophyllus*. A review of the literature relating to accessory transfusion tissue is to be found in Orr (15).

The single resin canal beneath the phloem varies considerably in size. It seems to be consistently small in *Podocarpus acutifolius*, large in *P. nivalis*, *P. gnidioides* and *P. alpinus*, but in *P. totara* and *P. hallii* it is found to vary from half the width of the vascular bundle to fully as wide.

The hypodermal fibers are mostly small. In *Podocarpus totara*, *P. hallii*, *P. nivalis* and *P. alpinus* they vary from 17–25 μ in diameter, seldom more than 15 μ in *P. acutifolius*, and often more than 30 μ in *P. gnidioides*. They are arranged in a single upper layer except at the margins in *P. acutifolius*. The layer is sometimes doubled and usually is interrupted in *P. alpinus* and *P. nivalis*, but mostly continuous in *P. totara* and *P. hallii*. Hypodermal fibers are found between the stomatal rows in all species but *P. gnidioides* and are most abundant in *P. totara* and *P. hallii*.

True fibers between the phloem and the resin canal were found in several leaves of *Podocarpus totara* and *P. alpinus*. Such fibers, however, are exceedingly rare in this subsection. In some of the other species, the mesophyll cells surrounding the vascular bundle seem to be differentiated in having denser cell contents or slightly thickened walls, but never by being enlarged.

The species in this group do not have bracts on the peduncle of the female cone below the receptacle, suggesting a closer relationship to subsection C in South America than to those species in the western south Pacific region. The single resin canal beneath the phloem is also characteristic of both subsections. Pilger (17) divides section *Eupodocarpus* into two subsections, A and B. In his subsection A he groups all the American species of *Eupodocarpus* and the species included in subsection D in this study.

Concentrated studies on the New Zealand conifers have been made and the polymorphism of many of them led to the early recognition and study of hybridization in the wild flora. This was found to account for the intergrading varieties between *Podocarpus totara* and *P. hallii*, two large trees, by Cockayne (6) and *P. hallii* and *P. nivalis*, a tall tree and a depressed shrub. A likely result of the latter cross may be *P. nivalis* var. *erectus* which has not yet been recognized as a hybrid. The former was named *P. × loderi* by Cockayne, but he considered it too early to present a definite name for the latter.

This subsection of *Eupodocarpus* has had the most extensive investigation of chromosome number (18). *Podocarpus acutifolius*, *P. alpinus* and *P. nivalis* agree with the other members of section *Eupodocarpus* in having $n = 19$. Burlingame is quoted as saying *P. hallii* has $n = 12$ but this bears reinvestigation as other counts made by this author have been incorrect.*

The taxonomy of *Podocarpus nubigenus* is not repeated in this paper as it was included with the species of section *Eupodocarpus* from South America (3).

KEY TO THE SPECIES OF SECTION EUPODOCARPUS, SUBSECTION D

Leaves pungent-mucronate; trees or shrubs.

Leaves 1–4 cm. (rarely 6 cm.) long; trees.

Leaves 2–3.5 mm. broad; bark thick; male flowers rarely solitary, sessile; seed obtuse *P. totara*.

Leaves 3–6.5 mm. broad; bark papery; male flowers solitary, peduncled; seed acute *P. hallii*.

Leaves 0.6–2.5 cm. long; shrubs.

Leaves thick, coriaceous; hypoderm interrupted; resin canal large.

* A recent communication from Dr. J. B. Hair, Crop Research Division, New Zealand, indicates that the chromosome counts of several of these species, when taken from native material, differ from the counts quoted above. He finds that the $2n$ chromosome number is 34 for *P. totara*, *P. hallii*, and *P. acutifolius*, 38 for *P. nivalis* and 36 for *P. nivalis* var. *erectus*.

- Prostrate branches; leaves not over 1.5 cm. long. *P. nivalis*.
 Erect branches; leaves up to 2.5 cm. long *P. nivalis* var. *erectus*.
 Leaves thin, coriaceous; hypoderm continuous; resin canal small.
 *P. acutifolius*.
 Leaves obtuse or rotundate at apex, not pungent; shrubs.
 Upper midrib of leaves flattened; pollen cones fascicled 3-6; hypoderm interrupted, single layer, fibers small *P. alpinus*.
 Upper midrib sulcate; pollen cones solitary; hypoderm continuous, doubled, fibers large *P. gnidioides*.

Podocarpus totara D. Don ex Lamb. Pinus ed. 2, 189. 1832; A. Cunn. in Ann. Nat. Hist. 1: 212. 1838 (excl. synonym.); D. Don ex Hooker in Lond. Jour. Bot. 1: 572. 1842; Raoul, Choix Pl. Nouv. Zél. 41. 1846; Endlicher, Syn. Conif. 212. 1847; Hooker f., Fl. Nov. Zealand 1: 233. 1853, Handb. N. Z. Fl. 258. 1864; Gordon, Pinetum 285. 1858, ed. 2, 350. 1875; Carrière, Traité Conif. ed. 2, 652. 1867 (excl. var.); Parlatore in DC. Prodr. 16: 514. 1868; Bertrand in Ann. Sci. Nat. ser. 5, 20: 59. 1874; Mahlerl in Bot. Centralbl. 24: 280. 1885; Kirk, Fl. N. Zealand 227. 1889; Kent in Veitch's Man. Conif. 153. 1900; Van Tieghem in Bull. Soc. Bot. France 38: 169. 1891; Pilger in Pflanzenreich IV. 5(Heft 18): 84. 1903, in Nat. Pflanzenfam. ed. 2, 13: 248. 1926; Cheeseman, Man. New Zealand Fl. ed. 1, 638. 1906, ed. 2, 111. 1925; Griffin in Trans. N.Z. Inst. 40: 43. 1907; Cockayne, Veg. N. Z. in Engler & Drude, Veg. der Erde, t. 28. 1921, t. 22. 1928; Bailey, Cult. Evergreens 180. 1923; Dallimore & Jackson, Handb. Conif. 56. 1923, 1931, 83. 1948; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 280. 1931; Laing & Blackwell, Pl. of N. Z. ed. 4, 66. 1940.

Podocarpus bidwillii Hoibrenk in Endlicher, Syn. Conif. 213. 1847.

Podocarpus cunninghamii Colenso, Visit to Ruahine Range 58. 1844.

A large tree, 10-30 m. or more high, trunk 0.5-2 m. in diameter, with thick bark; the short, sometimes thickly leafy branchlets scattered or subverticillate, green, scarcely ridged. Terminal buds 1.2-1.5 mm. wide, globose or ovate, with 2 series of bud scales usually sharply differentiated, the outer scales lanceolate, sometimes foliaceous, up to 3 mm. long, acute, attenuate, tips usually divaricate, green; inner imbricate, curving over growing tip, apiculate, ovate, brownish, margins scarious and erose. Leaves spreading scattered or arranged in 2 rows, 1-2 cm. long, 2.5-4 mm. wide, linear, rigid and coriaceous, very thick, pungent, narrowed at both ends, sharply pointed, straight or curved, sessile (juvenile leaves not essentially different); midrib not evident or only shallowly impressed above, clearer beneath. Pollen cones axillary, subsessile, fascicled 2 or 3, or at end of a short thick peduncle 1-2 mm. long (rarely solitary according to Kirk), base surrounded by stiff broad scales, erect, cylindrical, 1.5 cm. long, 3 mm. broad. Microsporophylls closely imbricate, rhomboidal, with a short obtuse apiculus, scarious margined, and sparingly denticulate. Female cones solitary, axillary, on short peduncles 2-3 mm. long; recep-

tacle of 2–4 fused fleshy scales, the upper ones not well developed, free at tip, subglobose and red when mature. Seeds 1 or 2 but usually solitary, small, subglobose, obtuse or rounded at apex, 10–12 mm. long.

DISTRIBUTION: New Zealand, on both North and South Islands, on slopes from sea level to 650 m., reaching largest size at 400 m. altitude. Not on Stewart Island.

In 1889, Kirk (14) distinguished *Podocarpus totara* from his new species, *P. hallii*, morphologically and geographically. In the former species the branchlets are always stiff and rigid, even in immature plants; the leaves do not differ in the young state from the mature leaves, the sessile male cones are rarely solitary and the seed is rounded at the apex and usually solitary. Thus he restricted the description somewhat from that of Pilger (16) which was written to include both species. In a short summary differentiating these two species, Kirk seems to have erred by reversing the mature leaf size which, for *P. totara*, is smaller in most cases, rarely exceeding 2 cm. in length and only reaching 3 mm. in width.

The cultivated specimen at Kew, known as *Podocarpus totara*, has rigid leaves which taper gradually toward the apex and suggest that it may rather be *P. hallii*, or a hybrid. UC10423, collected by Setchell in 1904, was determined by Cheeseman as *P. totara*, but it exceeds all specimens of this species seen in the size of the leaves.

There has been some minor confusion in the form of the name and its source. Don (10) first used the native name Totara to designate the species in 1832. Cunningham again described it in 1838 (8), calling it *Podocarpus totara*, the form used by New Zealand authorities Cockayne (6), Cheeseman (5), Kirk (14), and Pilger (17). The name is sometimes credited to A. Cunningham, but, following the International Code, it should be to D. Don as the earliest publication of the name.

SPECIMENS EXAMINED: *

NEW ZEALAND: North Island: Whangarei, *Kirk s.n.* (A, †F, †Mo, UC), *Kirk s.n.* (GH), *McLeod* in 1913 (†UC), *Cunningham 328* (TYPE) (†BR, K), Ruatangata, *Gordon* in 1910 (K—4 sheets); Bay of Islands, *Capt. Home s.n.* (†BM); *Matthews* in 1905 (†UC); Wellington, *Lawton s.n.* (†Ill). South Island: Otira Luga, *Kirk 467* (GH); Canterbury, *Adams* in 1914 (A); Woodbury, *Meebold 4059* (NY); Dunedin, *Meebold 4257* (NY); Mt. Martii, *Haast* in 1866 (†BR); Waya-runu Bay, U.S. So. Pac. Expl. Exped., *Anon.* in

* The following symbols indicate the herbaria of the specimens cited: Academy of Natural Sciences of Philadelphia (Ph), Arnold Arboretum (A), British Museum (BM), Brussels Botanical Garden (BR), University of California at Berkeley (UC) and at Los Angeles (LA), California Academy of Science (CAS), Chicago Natural History Museum (Field Museum) (F), Cornell University (CU), Gray Herbarium (GH), University of Illinois Herbarium (Ill), Royal Botanic Gardens, Kew, (K), Missouri Botanical Garden (Mo), New York Botanical Garden (NY), Paris Museum National d'Histoire Naturelle (P), Yale University Herbarium (YU).

† This symbol preceding the abbreviated name of an herbarium following the specimens examined signifies that the details of the leaves of this specimen have been examined in cross-section.

1838 (GH). LOCALITY NOT INDICATED: *Colenso* 1631 (K), *Colenso* for J. D. Hooker (K), *J. D. Hooker* (K), *Colenso s.n.* (K).

CULTIVATED: Hontika, *Wilson* in 1921 (A); England, Royal Botanic Garden at Kew, *Anon.* in 1857 (†Mo), *Cook* in 1937 (†Ill); Italy, Botanic Garden, Naples, H.13, *Cestai* to Engelmann in 1870 (†Mo—3 sheets), *Anon.* in 1868 (Mo); U.S. California, Golden Gate Park, *Collins* in 1918 (YU), *Eastwood* in 1913 (CAS), in 1914 (A), in 1916 (A—2 sheets, CAS), *Walther* in 1924 (A), *Buchholz* in 1942 (†Ill), Santa Barbara, *Van Rensselaer* 1725 (†Ill).

Podocarpus hallii Kirk, Forest Fl. N. Z. 13. 1889; Cheeseman, Man. N. Z. Fl. 648. 1906, ed. 2, 111. 1925; Cockayne, Veg. N. Z. in Engler & Drude, Die Veg. der Erde 111. 1921, 1928; Pilger in Nat. Pflanzenfam. ed. 2, 13: 247. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 279. 1931.

Podocarpus totara var. *hallii* (Kirk) Pilger in Pflanzenreich IV. 5(Heft 18): 84. 1903; Dallimore & Jackson, Handb. Conif. 57. 1923, 1931, 83. 1948.

A tall tree, 8–20 m. high, 0.5–1 m. in diameter, with thin papery bark; juvenile plants slender, the branchlets at right angles to main axis or often pendulous. Terminal buds slightly larger than twig, all scales broadly ovate, margins scarious and erose, obtuse and sometimes apiculate. Leaves on mature plants 2–4 cm. long, 1.5–3.5 mm. wide, linear, rigid, coriaceous, close-set in several series, erect, pale green when dry, narrowed at base into a very short flat petiole, tips pungent; midrib prominent beneath. Juvenile leaves 2-ranked, larger than mature leaves, 2–6.8 cm. long, 4–5 mm. wide, lanceolate, spreading, often abruptly narrowed at the base and very gradually narrowing to the apex. Pollen cones sessile, solitary (according to Kirk, 14) on distinctly stalked peduncle. Microsporophylls short, broad, apiculate. Female cones solitary on 2–3 mm. long peduncles; receptacle of 2–4 fused fleshy unequal scales free at acute tips, red at maturity, subglobose. Seed acute, pointed at apex, crested, often in 2's, 1–1.2 cm. long.

DISTRIBUTION: Endemic in New Zealand, most abundant on South Island and especially on Stewart Island, sea level to 950 m.

Several times the specific designation has been used in varietal status. Cheeseman (5), after listing it as a species, says "the variety designation might be right but the bark difference is significant." Pilger (16) lists, but questions, *Podocarpus laeta* Hoibrenk as a synonym of *P. totara* var. *hallii*. Endlicher (11) gives the locality for this species as New Holland (Australia) making the combination most improbable, and its correct position cannot be determined without the type specimen.

At the Royal Botanic Gardens, Kew, is an herbarium specimen said to be from a living specimen believed to be a hybrid of *Podocarpus hallii* and *P. nivalis* brought to Kew from Beech Forest, Bealey Valley, N. Z.*

* The living specimen was not seen in 1950 by Prof. Buchholz on his visit to the garden.

SPECIMENS EXAMINED:

NEW ZEALAND: North Island: Ruatangata, *Setchell* in 1904 (†UC-2 sheets); Kartaria, Mongonni Creek, Carse (K); Bay of Islands, U.S. So. Pac. Exped., *Anon.* (GH); Te Aroha, *Chase & Leland 276b* (†Mo); Ruahine Mts., *Tryon s.n.* (A); *Kirk s.n.* (A). South Island: Clinton Valley, *Cockayne 6648*, *Petrie* (NY); Dunedin, Leith Valley, *Lindsey* in 1935 (CU); Westport, *Townson s.n.* (K); Otira Gorge, *Oliver s.n.* (K). Stewart Island: *Cockayne 6661* (†F-2 sheets), *Kirk s.n.* (†F, GH, †Mo). LOCALITY NOT INDICATED: Flea Bay, *Karva* in 1910 (†A); ex Masters Herb., *Anon.* (K); *Morhange s.n.* (†BR); ex Prager Herb., *Anon.* (CAS); *Prince* in 1898 (GH).

CULTIVATED: England, Roy. Bot. Gard., Kew, *Cook* in 1937 (†III); Australia, *Hennings* in 1885 (Mo); U.S., California, Greendale, *Anon.* (A); Golden Gate Park, San Francisco, *Eastwood* in 1916 (CAS), in 1917 (CAS), *Walther* in 1921 (CAS), in 1923 (A), in 1924 (A).

Podocarpus nivalis Hooker, Icon, Pl. pl. 582. 1843; Raoul Choix Pl. Nouv. Zél. 41. 1846; Endlicher, Syn. Conif. 214. 1847; Hooker, f., Fl. N. Z. 232. 1853, Handb. N. Z. Fl. 257. 1864; Carrière, Traité Conif. ed. 2, 655. 1867; Parlature in DC. Prodr. 16: 519. 1868; Mahlert in Bot. Centralbl. 24: 280. 1885, Kirk, For. Fl. N. Z. 65. 1889; Pilger in Pflanzenreich IV. 5 (Heft 18): 85. 1903, in Nat. Pflanzenfam. ed. 2, 13: 247. 1926; Cheeseman, Man. N. Z. Fl. 649. 1906, 112. 1925; Cockayne, Veg. N. Z. 1921, 1928; Dallimore & Jackson, Handb. Conif. 53. 1923, 1931, 78. 1948; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 279. 1931; Laing & Blackwell, Pl. N. Z. 66. 1940.

Podocarpus montanus Colenso in Trans. N. Z. Inst. 27: 395. 1895.

A suberect shrub with numerous crowded, rigid branches, 0.5–2.5 m. high in sheltered situations or a low bush with spreading prostrate rigid branches which give off roots from the under surface in more open areas. Branchlets short, thickly leafy, ridged from pulvini at bases of sessile leaves and prominent leaf scars. Terminal buds globose with short greenish, broadly lanceolate, keeled, acute, scarious-margined, erose outer scales; on seedlings more ovate with triangular scales. Leaves vary in size, the larger in the middle of a growth period, thick and coriaceous, very stiff, linear, 0.9–1.5 cm. long, 2–2.5 mm. wide (2.5 cm. long on seedlings), patent, gradually narrowed to base, abruptly obtuse or acute at apex, mucronate, sessile or only very short stalked; midrib prominent below, stout, slightly impressed above giving a folded appearance; margin of blade thickened. Pollen cones fascicled, 2–4 at tip of common peduncle (sometimes solitary according to Dallimore & Jackson, 9), 3–5 mm. long, surrounded at base by minute stiff bracts decurrent on peduncle to leaves, narrowly cylindric, 1 cm. long. Microsporophylls closely imbricated, apiculus scarcely evident. Female cones solitary, axillary, peduncle very short, 1 mm. long, thick; receptacle of two fused fleshy scales free at the obtuse tips, 3–7 mm. long. Seed ovoid, obtusely crested, 5–6 mm. long.

DISTRIBUTION: Endemic on North and South Islands of New Zealand

but not on Stewart Island. Restricted to alpine and subalpine localities, 650–1800 m. altitude.

Podocarpus nivalis is locally known as the Alpine Totara. Its spreading branches are dense and produce a characteristic appearance in the low, thick and often very large amount of ground covered by a single plant.

SPECIMENS EXAMINED:

NEW ZEALAND: North Island: Mt. Ngauruhoe, *Cheeseman s.n.* (K); Ruahine Mts., *Tryon s.n.* (A, †LA); Ruapehu, *Meebold 17905* (NY), ex Masters Herb., *Anon.* (K–2 sheets); *Bidwell s.n.* (†K). South Island: Mt. Movatt, *Kirk 468* (GH); Hooker Valley, Mt. Cook Dist., *Cheeseman 186* (K); Greenstone Valley, Totago, *Haast 49* (K); near Brownings top, *Haast 67* (K); Mt. Whitnombur, *Haast 104* (K); Valley of Camerons near Hawthe Glacier, *Haast 105* (K); on Old Morarius, near Cumuo, *Haast 109* (K); Canterbury, *Haast 541* (K); Mt. Bruce, *Kirk s.n.* (A, †F, †Mo, NY); Arthur's Pass, Southern Alps, *Cockayne 6645* (†CAS, NY); Clarence Valley, *Hector s.n.* (GH); Mt. Martii, *Haast* in 1866 (†BR–2 sheets). LOCALITY NOT INDICATED: *Colenso 966, 991, 1552, s.n.* (K).

CULTIVATED: Wellington, *Gunn 226* (GH). South Island, Park Gardens, *Anderson 85* (†F), *86* (A, †Mo, NY, Ph, UC).

Podocarpus nivalis Hooker var. *erectus* Cockayne in Trans. N. Z. Inst. 48: 199. 1916; *Cheeseman*, Man. N. Z. Fl. 112. 1925.

An erect shrub, 1–2 m. high. Leaves larger, sometimes nearly 2.5 cm. in length. Otherwise like the species proper. This form is found in a restricted area on South Island, but also appears in cultivation.

DISTRIBUTION: South Island, 1000 m. on Mt. Owen and Mt. Percival in Nelson Province and Cass River, Canterbury.

SPECIMENS EXAMINED:

NEW ZEALAND: South Island: Mt. Sugarloaf, Cass, *Foweraker & Cockayne 20000* (TYPE) (†A–2 sheets); Southern Alps, Canterbury, Big Ben, *Cockayne 189* (†GH); Hermitage, Mt. Cook region, *W.A. & C. B. Setchell* in 1927 (UC); ?Bay of Islands, U.S. So. Pac. Expl. Exped., *Anon. s.n.* (GH).

CULTIVATED: California, Golden Gate Park, *Eastwood* in 1916 (CAS), *Walther* in 1920 (CAS), in 1923 (A), in 1924 (A), *Walker 5165* (UC).

Podocarpus acutifolius Kirk in Trans. New Zealand Inst. 16: 370. 1883, For. Fl. N. Z. 64. 1889; Pilger in Pflanzenreich IV. 5 (Heft 18): 84. 1903, in Nat. Pflanzenfam. ed. 2, 13: 247. 1926; Cockayne, Veg. N. Z. 1921, 1928; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 279. 1931.

Podocarpus parvifolius Parlatores in DC. Prodr. 16: 514. 1868; Dallimore & Jackson, Handb. Conif. 54. 1923, 1931, 79. 1948.

An erect-branched shrub, 1–2 m. high, branches short and rigid (in sheltered places slender), erect. Branchlets 1–1.2 mm. in diameter, green, ridged, leaf scars prominent. Terminal buds ovate, no wider than stem,

with scales lanceolate, attenuate, tip stiff and thick, base broad, with scarious erose margins. Leaves crowded (spreading and lax in sheltered places), thin, green, 1–1.5 cm., or more long, 1.5–2 mm. wide (rarely 2.5 mm.), coriaceous, narrow-linear, long-angustate, pungent; midrib prominent beneath, flat above; stomata in 2 whitish bands on underside. Pollen cones 1 or 2 (or more) fascicled on a short peduncle, each cone surrounded at base by 4 ovate acute-obtuse, broad, scarious-margined scales, 2.5 cm. long. Microsporophylls obtuse. Female cones solitary, axillary, on very short 1 mm. peduncles; receptacle of 2 or 3 fused unequal fleshy scales, the larger scale fertile, free at the obtuse tips, red. Seed narrow-ovoid, 4 mm. long, 3 mm. wide, crested.

DISTRIBUTION: Mountain districts in Marlborough, South Island. Known as the Acute-leaved Totara.

SPECIMENS EXAMINED:

NEW ZEALAND: South Island: Hope Valley, *Kirk s.n.* (A, †F, GH, †Mo); Canterbury, *Haast* in 1866 (†BR); Lake Rotoit, Nelson, *Cheeseman s.n.* (Ph.), *Anon.* ex Gordon Herb. (A); Lake Rolaiti, *Cheeseman s.n.* (K); Lake Brunner Dist., Westland, *Cockayne 6646* (A, NY); Glenhope, *Cockayne 8555* (A); Western Botanic Dist., near Waiko, *Cockayne 10022* (A–2 sheets); Omerva Saddle, *Cockayne 10020* (A); Mt. Duppa, Marlborough, *Sledge 247* (CU); Nothopip forest, Marcuia Valley, *Cockayne 13579* (K); ex Masters Herb., *Anon. s.n.* (K).

CULTIVATED: New Zealand: North Island, Ruatangata Garden, *Setchell* in 1904 (†UC, 1–2 yr. seedlings); South Island, Dunedin Botanic Garden, *Lindsey* in 1935 (CU–2 sheets). England: Kew, Royal Botanic Garden, *Cook* in 1937 (†III–2 sheets). United States: California, Golden Gate Park, *Eastwood* in 1916 (CAS), in 1919 (CAS), *Walther* in 1920 (†CAS), Greendale, *Anon. s.n.* (A).

Podocarpus alpinus R. Brown ex. Mirb. Geogr. Conif. in Mém. Mus. 13: 75. 1825 (nomen!); Bennett in Horsfield Pl. Jav. Rar. 40. 1838 (nomen!); Hooker f. in Lond. Jour. Bot. 4: 150. 1845, Fl. Tasmania 1: 356. 1860; Endlicher, Syn. Conif. 214. 1847; Parlatore in DC. Prodr. 16: 520. 1868; Bentham, Fl. Australia 6: 248. 1873; Mahlert in Bot. Centralbl. 24: 280. 1885; Kent in Veitch's Mar. Conif. 148. 1900; Pilger in Pflanzenreich IV. 5 (Heft 18): 83, f. 16E, 85. 1903, in Nat. Pflanzenfam. ed. 2, 13: 218, f. 117E, 247. 1926; Baker & Smith, Res. Pines of Australia 442. 1910; Dallimore & Jackson, Handb. Conif. 38. 1923, 1931, 60. 1948.

Nageia alpina F. Müller in Pap. Roy. Soc. Tasmania 23. 1879.

Podocarpus alpina var. *lawrencii* Hooker f., Fl. Tasmania 1: 356. 1860.

Podocarpus lawrencii Hooker f. in Lond. Jour. Bot. 4: 151. 1845.

Podocarpus totara var. *alpina* Carrière, Traité Conif. ed. 2, 652. 1867.

A low shrub up to 4 m. in height, densely branched; branchlets scattered, short, spreading, thickly leafy, greenish, ridged, with leaf scars raised on pulvini. Terminal buds ovate or globose, of the same diameter as the stem;

outer scales elongate, up to 2 mm. long, keeled, erect, tip thick and broad, becoming shorter with acuminate tip; inner scales thin, keeled, broadly triangular, brown, margins scarious and erose, short apiculate, often not deciduous. Leaves spreading, coriaceous, oblong-linear, shortly rotundate or obtuse at the tip, sometimes shortly subapiculate, gradually narrowing to the sessile base, 0.5–1.2 cm. long, 1.5–2.5 mm. broad; midrib flat or slightly impressed above, broad and prominent below. Pollen cones fascicled 3–6 (solitary and sessile according to Dallimore & Jackson, 9) at the tip of peduncles 3–4 mm. long (up to 1 cm.), in the axils of short scarious-margined bracts, these sometimes as long as the leaves, decurrent on peduncle, patent, cones 6 mm. long. Microsporophylls imbricate, crowded, triangular obtuse with fairly long apiculi. Female cones on very short peduncles or sessile; receptacle small, 3 mm. long, of two fused fleshy scales with rather long free tips. Seed ovoid, 5 mm. long (or less), crested.

DISTRIBUTION: High mountain regions in New South Wales of Australia and Tasmania.

SPECIMENS EXAMINED:

AUSTRALIA: New South Wales: Mt. Kosciusko, *Maiden & Forsyth* in 1899 (A, †CAS, †Mo, UC). Tasmania: Western Mts., *Rodway* in 1929 (†A); Mt. Field, east side, *Maiden* in 1906 (†A, †BR, GH); Mt. Wellington, *Gunn 226* (†GH, YU); Sasset, Border Hill, The Warren Wood, *Jackson* in 1936 (A); *Beunit 120* (TYPE) (†BM); *O.W.F. s.n.* (†BR); *Pibrin 4* (K); ex Gay Herb., *Anon. s.n.* (GH).

CULTIVATED: England: Kew, Royal Botanic Garden, *Nicholson 68* (A), *A.R.* in 1901 (A); ex Gordon Herb. *Anon. s.n.* (A). United States: California, Golden Gate Park, *Buchholz* in 1942 (†Ill).

Podocarpus gnidioides Carrière, *Traité Conif.* ed. 2, 656. 1867; Pilger in *Pflanzenreich IV. 5* (Heft 18): 82. 1903, in *Nat. Pflanzenfam.* ed. 2, 13: 84. 1926; Schlechter in *Bot. Jahrb.* 39: 16. 1907; Guillaumin in *Ann. Musée Col. Marseille* ser. 2, 9: 269. 1911, in *Bull. Mus. Hist. Nat. Paris* 18: 100. 1912, *Fl. France D'Outre-Mer* 10. 1948; Dallimore & Jackson, *Handb. Conif.* 46. 1923, 1931, 70. 1948; Florin in *Svenska Vet.-Akad. Handl.* ser. 3, 10: 279. 1931.

Podocarpus gnidioides var. *caespitosa* Carrière, *Traité Conif.* ed. 2, 656. 1867; Pilger in *Pflanzenreich IV. 5* (Heft 18): 84. 1903; Compton in *Jour. Linn. Soc.* 45: 426. 1922; Dallimore & Jackson, *Handb. Conif.* 46. 1923, 1931, 70. 1948.

Podocarpus alpina var. *aborescens* Brongniart & Gris in *Bull. Soc. Bot. France* 13: 425. 1866; Dallimore & Jackson, *Handb. Conif.* 46. 1923, 1931, 70. 1948.

Podocarpus alpina var. *caespitosa* Brongniart & Gris in *Bull. Soc. Bot. France* 13: 425. 1866.

A small shrub 0.5–2 m. high; branches decumbent, 1.2–1.5 mm. in diameter at tip, thickly leafy, green, ridged, with prominent leaf scars, the

bark becoming greyish, the inner bark brown. Terminal bud globose, flattened, 2 mm. in diameter, outer scales oblong or narrowly triangular, keeled, with thick tips erect or scarcely spreading, becoming shorter (1 mm. long), obtuse, with incurved tips; inner scales rotundate or broadly obtuse, scarious erose margined. Leaves quite spreading, linear, rounded to obtuse at the apex, sessile, gradually narrowing at the base, shiny above, very revolute margins when dry, 1.2–2 cm. long, 1–2 mm. broad; upper midrib shallowly grooved or abruptly sulcate, sometimes quite prominent below. Pollen cones axillary, solitary on peduncle 4 mm. long, erect, cylindric, surrounded at base by broad obtuse scales with scarious margins, 1–2 mm. long. Microsporophylls crowded, scarcely apiculate. Female cones solitary, axillary on short thick peduncle 1–1.5 mm. long; receptacle of 2 fused, almost equal, fleshy scales free at the broad obtuse tips, only 3–5 mm. long, bright red at maturity. Seed ovoid, crest erect, 5–7 mm. long, 3 mm. broad.

DISTRIBUTION: New Caledonia in summit flora of mountains.

SPECIMENS EXAMINED:

NEW CALEDONIA: Mt. Dore, *Pancher* 397 (P), *Pancher & Vieillard* 397 (P), *Pancher ex Thoret* (K), *Pancher s.n.* (P–3 sheets), *Pancher ex Hennecart* in 1879 (K, NY), *Vieillard* 3263 (P), *Viot* 209 (P–4 sheets), *Buchholz* 1432, 1433, 1435 (†Ill); Mt. Humboldt, *Viot* 343 (†P), *Viot* 422 (P), *Buchholz* 1575 (†Ill), *Schlechter* 15329, 15330 (†BR, K, P); Mt. Koghi, *Balansa* 183 (K, NY, P–4 sheets), *Franc* 2324 (A, P); Mt. Dzumac, *LeRat* 154, 330 (P), 2829 (K, P–2 sheets, *Franc* 532 (A, †BM, †LA, NY, P, †UC); Mt. Mou, *M. de Pompéry* in 1880 (P); Montagne des Sources, *MacDaniels s.n.* (†CU); Bourare, *Cribbs* 1183 (†P); Ile de Pins, *Jeanneney s.n.* (P). LOCALITY NOT INDICATED: *Muller* 70 (type coll., †P–2 sheets), *Muller s.n.* (P).

CULTIVATED: United States, California, *Buchholz* in 1942 (Ill).

Orr discusses *Podocarpus gnidioides* as a New Caledonian plant among the species in his geographical area (b) Asiatic, Malayan and Polynesian, but he emphasizes its relationship to the New Zealand species. He described the hypodermal fibers as “frequently superimposed on one another” and neatly packed together to “produce a characteristic mosaic appearance.” This is very striking and, on examination of transverse leaf sections, easily differentiates this species from the others in subsection D.

In 1866 Brongniart and Gris (1) described a tree which they called *Podocarpus alpina* var. *arborescens* from a *Muller* specimen collected in 1862. At the same time they described the shrub from Mt. Dore, New Caledonia, and named it *P. alpina* var. *caespitosus*. In the Paris Museum there now exist two similar *Muller* specimens, both #70. The herbarium labels of these give both Australia and New Caledonia as collection regions and one describes the plant as a “taxad” tree, 40 ft. high, with the habit of a *Sequoia*. It is a sterile specimen and a tag on it says “like *Taxus* New Cal.” The other #70 does not indicate habit. After almost a century, in which many collectors, notably *Pancher* and *Vieillard*, and in recent years *Compton*, *Buchholz*, *Chevalier* and others have made extensive

collections on New Caledonia, such a tree has not been seen again. I have examined the leaf anatomy of the first of the *Muller* specimens and do not observe any difference from that found in a large number of shrubby specimens from different mountain regions in New Caledonia. It is always characteristic. Compton (7) indicated that he could not find any difference in the external appearance of the foliage. It is now doubtful if it ever existed as a tree and it is probable that there was some confusion at the time labels were attached to the specimens.

Carrière (4) recognized the tree and the shrub as a distinct species from *Podocarpus alpinus*, naming them *P. gnidioides* with a variety *caespitosus*. Unfortunately he selected the now doubtful tree for the type and made the shrub the variety. The life history of the shrub is completely known. Since the tree habit is the only vegetative difference, buds, twigs, and leaves all being the same, it now seems most desirable to omit from the description the existence of a tree except as a mere possibility. Prof. Buchholz, when pursuing his extensive studies of New Caledonian conifers, reached the decision to drop the use of the variety *caespitosus*. This is consistent with the rules of nomenclature in that *Muller* #70 is obviously the type of *P. gnidioides* and it is identical with the plant we now know.

LITERATURE CITED

1. BRONGNIART, A. AND A. GRIS. Sur quelques Conifères de la Nouvelle-Calédonie. Bull. Bot. Soc. France 13: 422-427. 1866.
2. BUCHHOLZ, JOHN T. AND NETTA E. GRAY. A taxonomic revision of Podocarpus. I. The sections of the genus and their subdivisions with special reference to leaf anatomy. Jour. Arnold Arb. 29: 49-63. 1948.
3. ——— AND ———. A taxonomic revision of Podocarpus. IV. The American species of section Eupodocarpus, subsections C and D. Jour. Arnold Arb. 29: 123-151. 1948.
4. CARRIÈRE, E. A. Traité Coniferae, ed. 2, 1867.
5. CHEESEMAN, T. F. Manual of New Zealand Flora. 1925.
6. COCKAYNE, L. Polymorphism in New Zealand conifers. Conifers in Cultivation (Rep. Conifer Conference, Nov. 1931) 151-164. 1932.
7. COMPTON, R. H. Gymnosperms. Linn. Soc. Jour. Bot. 45: 421-434. 1922.
8. CUNNINGHAM, ALLAN. Florae Insularum Novae Zelandiae Precursor. Ann. Nat. Hist. 210-216. 1838.
9. DALLIMORE, W. AND A. BRUCE JACKSON. A Handbook of Coniferae, ed. 4, 1948.
10. DON, D. Podocarpus. Lambert's Pinus, ed. 2, 189. 1832.
11. ENDLICHER, S. Synopsis Coniferarum. 1847.
12. GRIFFIN, E. M. Conifer leaves with regard to transfusion tissue and to adaptation to environment. Trans. New Zealand Inst. 40: 43-72. 1907.
13. GRIFFITH, MILDRED M. The ontogeny of transfusion tissue in the leaf of Podocarpus. Paper presented at the annual meeting of the Assoc. South-eastern Biologists, Louisiana State Univ. in April, 1954.

14. KIRK, THOMAS. Forest Flora of New Zealand. 1889.
15. ORR, M. Y. The leaf anatomy of Podocarpus. Trans. Bot. Soc. Edinburgh 34: 1-54. 1944.
16. PILGER, R. Taxaceae. Pflanzenreich IV. 5 (Heft 18): 1-124. 1903.
17. ———. Podocarpaceae. Nat. Pflanzenfamilien, ed. 2, 13: 211-249. 1926.
18. STIFF, McHENRY L. The geographical distribution and cytology of the Coniferales. Ph.D. Thesis, Univ. of Virginia, 1952.

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PHLOEM POLARITY IN BARK REGENERATION¹

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THE POLARITY of phloem transport is the basis for checking tree growth by inverting a ring of bark on the trunk of the tree (7). If a ring of bark is removed, turned upside down and held firmly against the xylem with a rubber band, it will reunite with the wood. The inverted ring of bark will continue to form xylem, but the growth is slow, due to the checking of phloem transport by the reversed polarity. The bark formed at the vertical seam of the inverted ring does, however, make normal growth, presumably due to its normal polarity. As a result the dwarfing effect of the inverted ring of bark is temporary, because normal phloem transport is soon established in the bark regenerated at the vertical seam.

In order to test the origin of the regenerated bark at the vertical seam of a ring of bark grafted on a woody stem we grafted a ring of bark from an apple tree with red wood and bark onto an apple tree with white wood and green bark. In the first experiment the ring of red bark was grafted in the normal position in early June. By the end of the growing season it was evident that the new wood formed beneath the ring of red bark was red, but that the wood formed at the vertical seam was white. Obviously the new wood and bark was derived from the regeneration of the underlying xylem elements rather than from the adjacent bark. The growth of xylem was essentially the same whether derived from the regenerated bark or from the ring of red bark, as is shown in FIGURE 1.

In the second experiment a ring of red bark was grafted, upside down, on a branch with white wood. The xylem formed under the red bark was red, but there was comparatively little wood formation under the ring of red bark as is shown in FIGURE 2. The wood formed at the vertical seam was white and made essentially normal growth. It is evident that the cambium regenerated at the vertical seam is derived from the underlying wood and not from the cambium of the adjacent bark. It is also evident that the growth of the xylem at the vertical seam is normal, regardless of the orientation of the adjacent bark. The growth of the xylem beneath the inverted ring of bark is, however, greatly suppressed, presumably because of the reversed polarity of the phloem.

The polarity of phloem regenerated from the surface of the xylem does not appear to be determined by the orientation of the adjacent cambium yet the adjacent cambium seems to play a role in the formation of new cambium. In *Hibiscus*, according to Sharples and Gunnery, the exposed wood, following removal of the bark, produces large thin walled cells derived from the ends of the medullary rays and smaller cells from meristematic cells which are normally destined to form xylem. If kept moist these cells form a parenchymatous cushion about a millimeter deep in two or

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three weeks. New cambium is then formed across the callus cushion, beginning where the callus is in contact with the cambium of the adjacent bark and "like a slowly closing diaphragm sweeps gradually inward until opposing edges meet. . ." (8). The cambium then produces new wood and bark.

According to Sharples and Gunnery both bark callus and wood callus are formed largely from medullary ray elements. Since the medullary rays are oriented across the long axis of the stem and pass from the xylem through the cambium to the phloem they would not be expected to be polarized in a vertical direction. How then does the phloem derived largely from medullary ray elements become normally polarized? Sharples and Gunnery observed that "new cambial elements do not appear except in close proximity to pre-existing cambial elements" yet the polarity of the resulting phloem cells do not appear to be influenced by the adjacent inverted cambium.

In order to further test the effect of adjacent cambial tissue on the orientation of regenerated phloem and xylem an experiment was designed based upon a technique described by Garner (1). Squares of bark a little more than an inch in diameter were removed from young apple trees with white wood, and replaced with squares of bark from apple trees with red wood. A smaller square of bark about a third of an inch in diameter was removed from the center of each of the red squares leaving the white wood exposed, surrounded on all sides by red bark. The grafts were covered with polyethylene film to keep the exposed wood moist, and the grafted bark was bound firmly with a rubber band until it was united with the wood.

The blocks of red bark were oriented in the normal position, upside down and laterally on the white wood. At the end of the growing season the grafts were removed and sectioned. As shown in FIGURE 3 the normally oriented graft made much more growth, both of the wood beneath the red bark and that from the regenerated cambium, than those in the inverted (FIG. 4) or transverse (FIG. 5) position. In all cases, however, the regenerated xylem was oriented in a vertical position, regardless of the orientation of the grafted square of red bark (FIG. 6). It is evident that the orientation of the cambium regenerated from the white wood is not determined by the orientation of the adjacent cambium.

When the grafted bark is oriented in a normal position there is only a slight overgrowth of the normal tissue above the graft and a comparatively uniform growth of the grafted bark along its entire length as is shown in FIGURE 3. Such a uniform growth would be expected if normal phloem transport in the graft were soon established. However, when the grafted bark is oriented in an inverted or transverse position, there is considerable swelling of the normal tissue above the graft and differential growth in the grafted bark as is shown in FIGURES 4 and 5. The swelling above these grafts can be attributed to the blocking of normal phloem transport and the resulting accumulation of nutrients and hormones above the graft. The differential growth within the length of the graft can be attributed to the diffusion of nutrients and hormones accumulated above the graft. The diffusion must be slow because the growth of the inverted or transverse graft

is greatly reduced, but the greater growth at the upper end of the grafted bark indicates that some nutrients are diffused into this tissue. This greater growth at the upper junction of the graft (A, Figs. 4 and 5) can not be attributed to growth stimulation by "wound hormones," because no such differential growth is found at the lower end of the graft union, either at the union between the abnormally oriented bark and the upper end of the regenerated bark (B, Figs. 4 and 5), or between the transverse or inverted bark and the lower union with the normal bark (D). There is, however, a secondary swelling at the junction of the lower end of the regenerated bark and the abnormally oriented bark (C). Apparently the diffusion of nutrients continues down the inverted or transverse bark to some extent and the nutrient sap passes freely into the regenerated bark, since the regenerated bark is normally polarized. But when it reaches the base of the regenerated bark it must then pass by diffusion into the inverted or transverse grafted bark and tends to accumulate and promote increased growth at the upper end of the abnormally oriented bark. The growth in this region is much less than at the upper junction of the graft because the nutrients have been greatly diminished by blocking of phloem transport in the upper part of the graft.

The inversion of a ring of bark on the trunk of the tree suppresses growth by checking phloem transport down the trunk of the tree and thus decreasing the flow of organic nutrients to the roots. The effect of the bark inversion is temporary, however, due to the regeneration of normally polarized phloem and xylem. If a single ring inversion is made, the normally polarized elements regenerated at the vertical seam grow so rapidly that the dwarfing effect of the inverted ring of bark is soon lost, especially in young vigorous trees. We have attempted to avoid this restoration of normal phloem transport by using two inversions with the vertical seams on the opposite side of the trunk of the tree. Restoration of normal transport is delayed, but not prevented, by this technique.

When a second inverted ring of bark is grafted directly above the first one, the growth of the tree is checked for several year. The descending sap moves down the phloem regenerated at the first vertical seam, but is checked by the second inverted ring of bark. There is, however, a lateral movement of the nutrient sap, particularly in the lower inverted ring of bark, so that eventually it makes contact with the regenerated phloem of the lower vertical seam on the opposite side of the trunk of the tree. This lateral diffusion of sap is followed by a lateral orientation of the new phloem and xylem. Eventually normal phloem transport is established down the regenerated phloem at the first vertical seam and then laterally across the lower end of the upper inversion, and the upper end of the lower inversion, to the regenerated phloem at the second vertical seam and then on down the stem.

When the two inversions are made with a ring of normal bark between them the nutrient sap descends the regenerated phloem at the vertical seam of the first inversion, but can pass by lateral diffusion across the ring of normal bark to the upper end of the regenerated phloem of the seam of the second inversion. The xylem and phloem of the normal ring of bark

soon become oriented transversely at a downward angle to establish a continuity of normal phloem transport. Such a double bark inversion was made on a young poplar tree in June. At the end of the growing season the bark was removed to show how the xylem had grown at the vertical seams on opposite sides of the trunk and were connected by reoriented xylem

DESCRIPTION OF FIGURES

FIGURE 1. Cross section of an apple branch with white wood on which was grafted, in June, a ring of bark from an apple tree with red wood. At the end of the growing season the sectioned stem showed that the red bark had produced a normal growth of red wood beneath it. The wood produced at the vertical seam was white, proving that this bark and wood was regenerated from the surface of the white wood and not from the adjacent red bark.

FIGURE 2. Cross section of a ring of red bark grafted in an inverted position on an apple stem with white wood. At the end of the growing season the inverted ring of bark had produced little red wood, due to the reversed polarity of the phloem. The regenerated white wood made normal growth, indicating that the phloem regenerated from the white wood was normally polarized.

FIGURE 3. Longitudinal sections of an apple stem with white wood on which had been grafted a square of red bark after removing a small square of bark from the center of the red bark. The wood developed under the red bark was red and that regenerated from the exposed white wood in the center was white. When the red bark is grafted in the normal position the growth of the underlying red wood and of the regenerated white wood in the center is essentially normal.

FIGURE 4. Same as above, but red bark inverted. The growth of the wood, both under the red bark and under the regenerated bark is greatly reduced, due to blocking of phloem transport by the reversed polarity of the phloem of the grafted red bark. There is evidence of diffusion of nutrient sap into the grafted tissue as indicated by greater growth of wood at the upper end of the graft.

FIGURE 5. Same as above, but with grafted bark oriented in a transverse position.

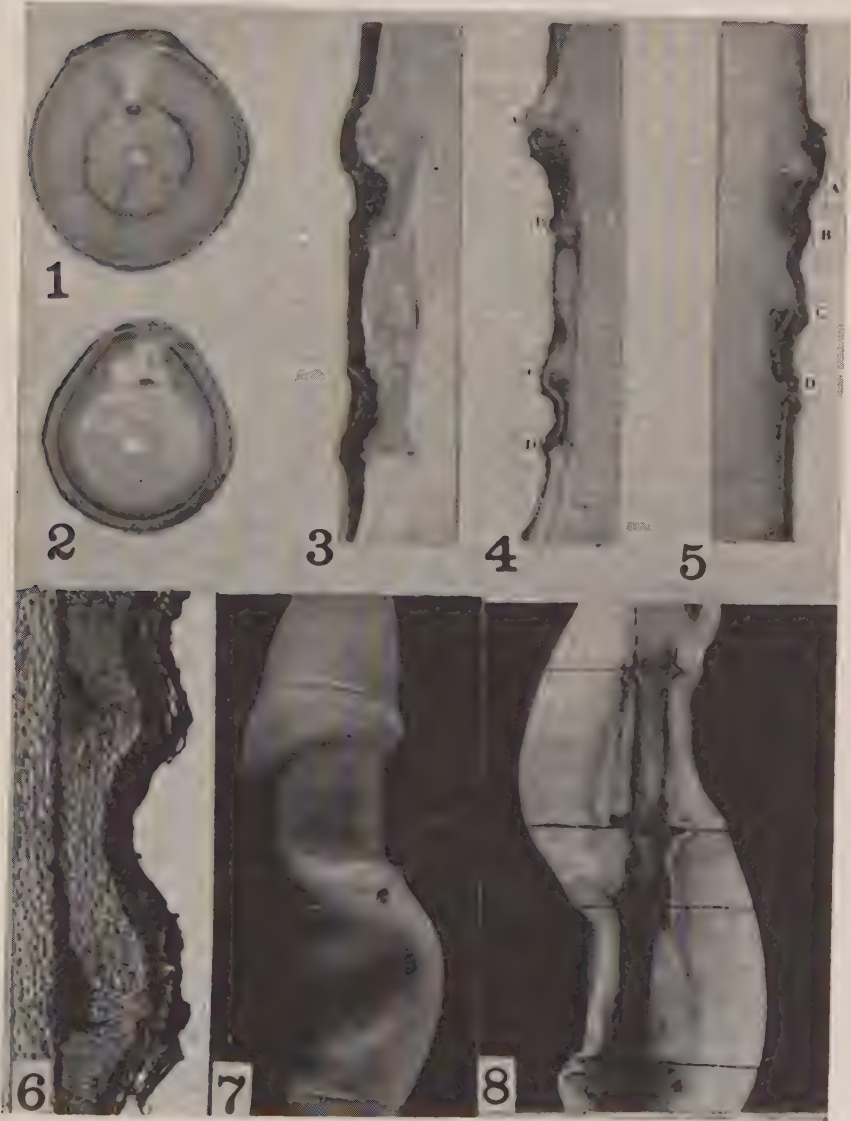
FIGURE 6. An enlarged section of the graft shown in FIG. 5. The red xylem is oriented transversely, but the xylem produced by the cambium from the tissue regenerated from the exposed white wood is normally oriented.

FIGURE 7. Orientation of xylem of a poplar stem at end of growing season after making a double bark inversion in June. The two bark inversions, with their vertical seams on opposite sides of the stem, were separated by a ring of normal bark. The regenerated bark at the vertical seam was normally polarized, permitting normal phloem transport. The nutrient sap descended the phloem of the upper regenerated bark at the seam, diffused laterally across the ring of normal bark and down the normally polarized seam of the lower inverted ring of bark. The lateral diffusion of the sap across the normal ring of bark was followed by a reorientation of phloem and xylem, establishing normal phloem transport and normal xylem growth by the end of the season.

FIGURE 8. Longitudinal section of a poplar stem following a double bark inversion as described for FIG. 7. Note greatly restricted growth of xylem beneath the inverted rings of bark, due to reversed phloem polarity.

across the stem under the normal ring of bark between the two inversions (Fig. 7). A longitudinal section of a poplar stem subjected to the same type of double bark inversion is shown in FIGURE 8.

The regeneration of new bark from exposed wood and the reorientation of the xylem and phloem has long been known. Thomas Andrew Knight in 1807 (3) referred to the work of Henri Louis Duhamel done more than



SAX & DICKSON — FIGURES

fifty years earlier. If a piece of bark is removed from a tree and the exposed wood is kept moist, "a glaucous fluid exudes from the surface of the alburnum; this fluid appears to change into a pulpy mass, which subsequently becomes organized into cellular matter. . .". A more modern and detailed description of this process was described by Sharples and Gunnery in 1933 (8).

Knight was also aware of the origin of new wood formed beneath a strip of grafted bark. In 1808 he wrote as follows: "Having procured, by grafting, several trees of a variety of apple and crab tree, the woods of which are distinguishable from each other by their colours, I took off, early in the spring, portions of bark of equal length, from branches of equal size, and I transposed these pieces of bark, inclosing a part of the stem of the apple with a covering of bark from the crab tree, which extended quite around it and applying the bark of the apple tree to the stem of the crab in the same manner. . . . A vital union soon took place between the transposed pieces of bark and the alburnum . . . and in the autumn it appeared evident that a layer of alburnum had been, in every instance, formed beneath the transposed pieces of bark." (4).

The reorientation of newly generated xylem and phloem was also observed by Knight (3). He found that the new vessels "may be made, by appropriate management, to traverse the new cellular substance in almost any direction," by controlling the direction of flow of the nutrient sap. In 1862 Hartig (2) described the reorientation of the xylem in the new wood developed above a spiral deletion of a strip of bark. These and other experiments, which show that the direction of flow of the nutrient sap controls the orientation of the newly formed xylem and phloem, have been described more recently, and in more detail, by MacDaniels and Curtis (6). The vessels gradually become reoriented so that they are parallel with the spiral.

SUMMARY

The inversion of a ring of bark on the trunk of a tree results in checking phloem transport to the roots and dwarfing the tree. The effect is not permanent because the new bark regenerated at the vertical seam is normally polarized and permits normal phloem transport. By grafting a ring of bark from an apple tree with red wood on a tree with white wood, it has been shown that the new bark and wood regenerated at the vertical seam of the grafted ring of bark is derived from the underlying wood and not from the adjacent bark.

A double bark inversion, with the vertical seams on the opposite sides of the trunk, increases the duration of the dwarfing effect, but the lateral diffusion of nutrient sap soon results in a lateral orientation of the new xylem and phloem, to bridge the normally polarized tissues regenerated at the seams of the two inverted rings of bark.

The nutrient sap may diffuse laterally or vertically if normal phloem transport is checked.

If a strip of bark is removed from a tree, the exposed wood, if kept moist, will regenerate new bark and wood. It is shown that the new cambium is oriented in the long axis of the stem, regardless of the orientation of the surrounding grafted bark.

The general conception of the regeneration of new growth from exposed wood, and the control of the orientation of xylem and phloem by the direction of flow of nutrients, dates back to the work of Knight early in the 19th century. These ideas, supplemented by more detailed analyses in later years, are of value in designing experiments dealing with the practical problems of controlling tree growth.

LITERATURE CITED

1. GARNER, R. J. *The Grafters Handbook*. Faber and Faber Ltd. London. 1947.
2. HARTIG, TH. Ueber die Bewegung des Saftes in den Holzpflanzen. *Bot. Zeit.* 20: 81-87. 1862.
3. KNIGHT, THOMAS ANDREW. On the formation of the bark of trees. Royal Society of London. *Phil. Trans.* 103-113. 1807.
4. ———. *Physiological and Horticultural Papers*. Longman, Orne, Brown, Green and Longman, London. 1841.
5. ———. Physiological observations upon the effects of partial decortication, or ringing of the stems or branches of fruit trees. *Trans. Hort. Soc. London.* 4: 159-162. 1820.
6. MACDANIELS, L. H. AND CURTIS, O. F. The effect of spiral ringing on solute translocation and the structure of the regenerated tissues of the apple. *Cornell Univ. Agr. Exp. Sta. Memoir* 133: 3-31. 1930.
7. SAX, KARL. The control of tree growth by phloem blocks. *Jour. Arnold Arboretum.* 35: 251-258. 1954.
8. SHARPLES, A. AND GUNNERY, H. Callus formation in *Hibiscus Rosa-sinensis* L. and *Hevea brasiliensis* Müll. *Arg. Ann. Bot.* 47: 827-840. 1933.

NEW SPECIES IN THE BAMBOO GENUS *PHYLLOSTACHYS* AND SOME NOMENCLATURAL NOTES

F. A. McCLURE¹

IN 1945 eight new species of the genus *Phyllostachys* were described² from the collection of living plants maintained by the U. S. Department of Agriculture at one of its field stations, the Barbour Lathrop Plant Introduction Garden, near Savannah, Georgia. Since that time, among the phyllostachid bamboos growing there, four additional species presumed to be new to science have advanced sufficiently in their development toward maturity to show characteristics of a distinctive nature. The following Latin descriptions³ were prepared on the basis of living plants growing under the respective U. S. D. A. Plant Introduction numbers cited. Type specimens are deposited in the U. S. National Herbarium, duplicates in the herbarium of the National Arboretum.

Phyllostachys bissetii McClure sp. nov.

FIG. 1.

Culmi usque ad 6.75 m. alti et 25 mm. diametro; *internodia* viridia usque ad 33 cm. longa (in culmo 6.75 m. alto, ut exemplo electo, internodio duodecimo maximo longitudine) omnia glabra vel inferiora saepius sursum setis erectis brevissimis parce sparsa, delapsis tegentibus vaginis laxae pruinosa; *nodi* pulvino cicatriceque modice et subaequaliter eminentes, cicatrice glabra. *Culmi vaginae* ad apicem truncatum sensim rotundatae vel angustatae, dorso glabrae (inferiores tantum primo interdum dorso pubescentes marginibus ciliatae) virides saepe vino passim tinctae haud maculatae; *auriculae* plus minusve valde evolutae (ambae alterutra interdum obsoletae) ovatae vel oblongae vel late falcatae margine *setis* rigidis scabris radiatim dispositis munitae; *ligula* brevis vino tincta, apice leviter convexa, margine plus minusve asymmetrica, setis hispidis albidis fimbriata; *vaginarum laminae* infimae anguste subtriangulae superiores gradatim usque ad formam lineari-lanceolatum mutantes, apice naviculiformes, inferiores appressae vel raro valde reflexae, superiores plus minusve patentes. *Foliorum vaginae* nonnullae auriculatae; *auriculae* margine setis radiatim fimbriatae; *ligula* modice evoluta; *foliorum laminae* lanceolatae vel oblongo-lanceolatae, subtus sparsim et invalide scabrae. *Inflorescentiae* desunt.

¹ Plant Introduction Section, Horticultural Crops Research Branch, Agricultural Research Service, U. S. Department of Agriculture.

² McClure, F. A. The vegetative characters of the bamboo genus *Phyllostachys* and descriptions of eight new species introduced from China. Wash. Acad. Sci. J. 35: 276-293. 1945. (Sept. 15).

³ A field manual under preparation will provide English descriptions and a field key for the identification of all of the bamboos of this genus known to be under cultivation in the Western Hemisphere.

Type in U. S. National Herbarium, Nos. 2177861-2 (2 sheets), collected by *F. A. McClure* (No. 21801), April 22, 1955 at the U. S. Barbour Lathrop Plant Introduction Garden where the plant is cultivated under P. I. 143540. The description is based on the living plants in a colony about 13 years old. Propagating material of this bamboo, from plants under cultivation at Chengtu, Szechwan province, China, was secured by John Tee-Van and brought to this country late in 1941 for the Plant Introduction Section of the U. S. Department of Agriculture.

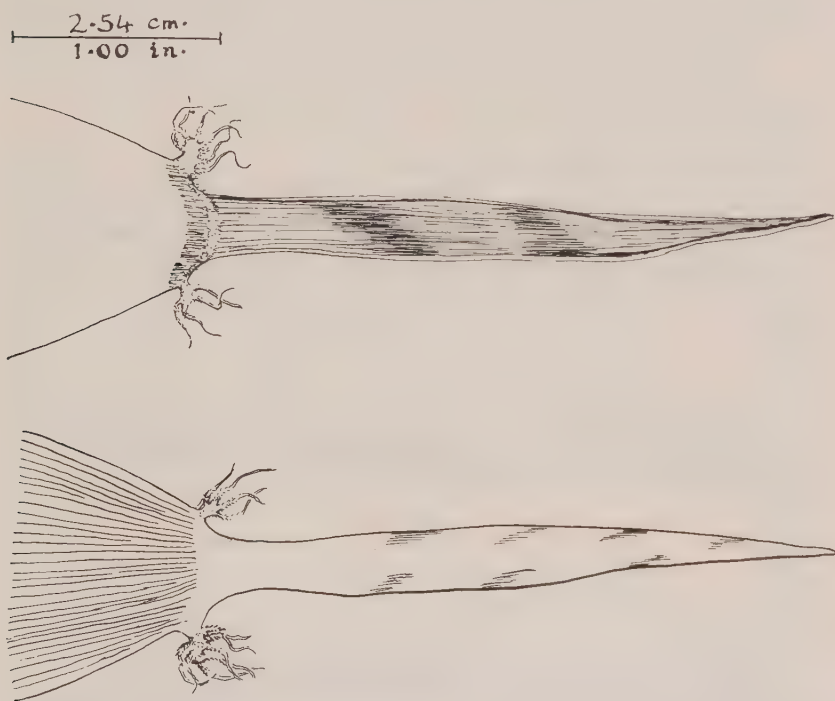


FIG. 1. *Phyllostachys bisetii* McClure sp. nov. Inner (above) and outer aspects of the apex of a mid-culm sheath.

The specific epithet signalizes the outstanding contribution to the development of popular interest in bamboo culture and utilization made by David Bisset as Superintendent of the U. S. Barbour Lathrop Plant Introduction Garden.

Phyllostachys bisetii is in some respects rather similar to *Ph. aureosulcata*, from which it is distinguished by the very sparse instead of dense pubescence of the lower internodes of the culms, by its lack of sharply defined color-stripping in the culm sheaths, and by minor differences in the shape of the apical structure of the culm sheaths. Moreover it lacks the yellow color-panel on the groove, a stable feature characteristic of the

internodes of young culms of *Ph. aureosulcata*. *Phyllostachys bissetii* is one of the first to initiate the growth of new shoots in spring. According to Mr. Bisset, it has shown signs of being one of the hardiest of the phyllostachids under observation at the Barbour Lathrop Garden.

In 1941, during the course of the New York Zoological Society's expedition to Australia and China, of which he was the leader, Mr. Tee-Van received two young Giant Pandas as a gift from the Chinese people to the American people. During their long voyage across the Pacific, these animals were fed with leafy branches of this bamboo and several other kinds. However, the bamboo on which the Giant Panda is known to feed in its native habitat is another species, a member of the genus *Sinarundinaria*. Unfortunately plants of the latter species introduced by Mr. Tee-Van at the same time did not survive.

***Phyllostachys decora* McClure sp. nov.**

FIG. 2.

Culmi usque et ultra 7 m. alti et 30 mm. diametro, virides, delapsis tegentibus vaginis nodis et internodiis sursum primiter setis perbrevis retrorsis sparsim scabris deinde sensim glabrescentibus, primo haud vel

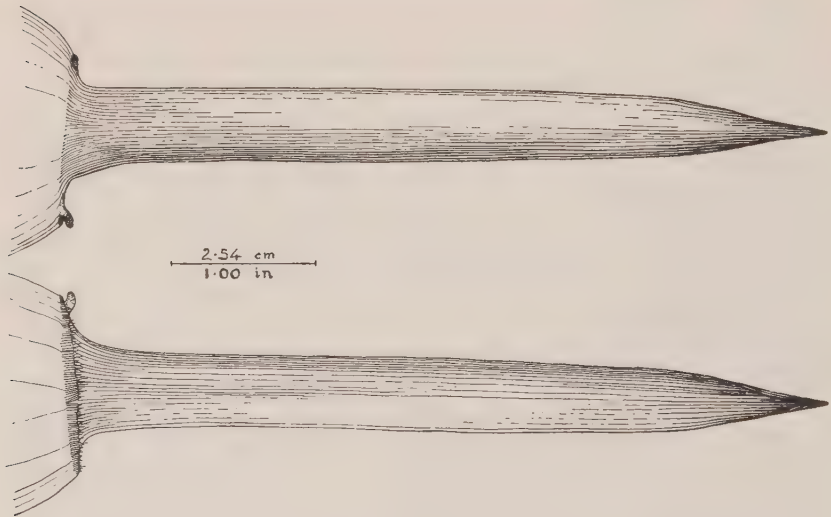


FIG. 2. *Phyllostachys decora* McClure sp. nov. Inner (below) and outer aspects of apex of a mid-culm sheath.

leviter glaucescentibus deinde sub nodos dense pruinosi; *internodia* interdum leviter striata, usque ad 15.8 cm. longa (in culmo 7.2 m. alto, ut exemplo electo, internodio undecimo maximo longitudine); *nodi* pulvino cicatriceque modice et subaequaliter eminentes, cicatrice glabra. *Culmi vaginae* ad apicem latum truncatumque subito rotundatae dorso glabrae haud pruinosaе, immaculatae vel maculis minutis fuscis sparsim maculatae,

et porro colore saturato-viridi, viridi pallidiori alboque in longitudinem variegatae, interdum omnino paene albae, secundum margine purpura notatae; *auriculae* 1 vel 2 vel nullae, variabiles, angustatae falcatae fuscae nudaе vel setis paucis invalidis fuscis margine fimbriatae; *ligula* primiter purpurata latissima et comparate brevis, apice truncata vel leviter undulata vel invalide convexa margine ciliis albis et setis crassis scabris fuscis fimbriata; *vaginarum laminae* late lanceolatae usque ad liguliformes, apice subito acutae, infimae appressae superiores appressae vel plus minusve patentem interdum invalide undulatae. *Foliorum vaginae* invalide auriculatae, *auriculis* plerisque parvis saepe obsoletis; *setae orales* paucae fragiles et fugaces; *ligula* vix exserta primiter purpurata; *foliorum laminae* subtus invalide et sparsim scabrae.

Type in U. S. National Herbarium, Nos. 2177856–8 (3 sheets), collected by F. A. McClure (No. 21757), April 16, 1953, from a colony cultivated under P. I. 128789 at the U. S. Barbour Lathrop Plant Introduction Garden. The description is based on the living plants in a colony about 15 years old.

Plants of this bamboo from the Hoi Wai Monastery, Lung Chi Mt., near I-Ming, Kiangsu province, China, where it is known by the Chinese (National) vernacular name *Mei Chu* (Beautiful Bamboo), were sent by the writer to the U. S. Department of Agriculture in 1938.

This species is readily distinguished from all the others of which the vegetative characteristics are known by the broad, truncate apex of the culm sheath and the broad but short purple ligule exerted on each side of the strap-shaped sheath blade.

Phyllostachys elegans McClure sp. nov.

FIG. 3

Culmi usque paene ad 10 m. alto et 54 mm. diametro, omnino glabri; *internodia* viridia inferiora comparate breviora, superiora usque et ultra 30 cm. longa (in culmo 9.88 m. alto, ut exemplo electo, internodio vicesimo primo maximo longitudine) graciliter striata, primiter laxae et copiose pruinosa; *nodi* pulvino colorato et cicatrice glabra modice et subaequaliter eminentes. *Culmi vaginae* versus apicem angustum sensim angustatae, dorso glabrae vel interdum in lateribus scabrae vel sparsim setosae, marginibus glabrae vel subtiliter ciliolatae, primiter omnino manifeste pruinosa, dilute luteo-virides, secundum nervos purpura laeviter tinctae et porro maculis parvis fuscis discretis vel in lineis directis junctis dorso omnino notatae; *auriculae* ambae alterutra nunc defectae nunc valde evolutae, falcatae, apicem tantum secundum marginem crebre dispositis *setis* longis curvis munitae; *ligula* apice convexiuscula, comparate angusta, ca. 2 mm. alta demptis *setis* marginalibus, margine undulato *setis* pallidis crassis subglabris fimbriata; *vaginarum laminae angustae* liguliformes canaliculatae apice attenuatae pleraeque valde crispae et reflexae. *Foliorum vaginae* vulgo auriculatae; *auriculae* margine *setis* oralibus munitae; *ligula* exserta vulgo purpurata; *foliorum laminae* late lanceolatae basi rotundatae

apice abrupte acuminatae, vulgo 100×17 mm. interdum usque ad 180×22 mm., subtus ubique dense puberulae.

Type in U. S. National Herbarium, Nos. 2177863-4 (2 sheets) collected by *F. A. McClure* (No. 21802), April 24, 1955, from the colony cultivated under P. I. 128778 at the U. S. Barbour Lathrop Plant Introduction Garden. The description is based on the living plants in a colony about 15 years old.

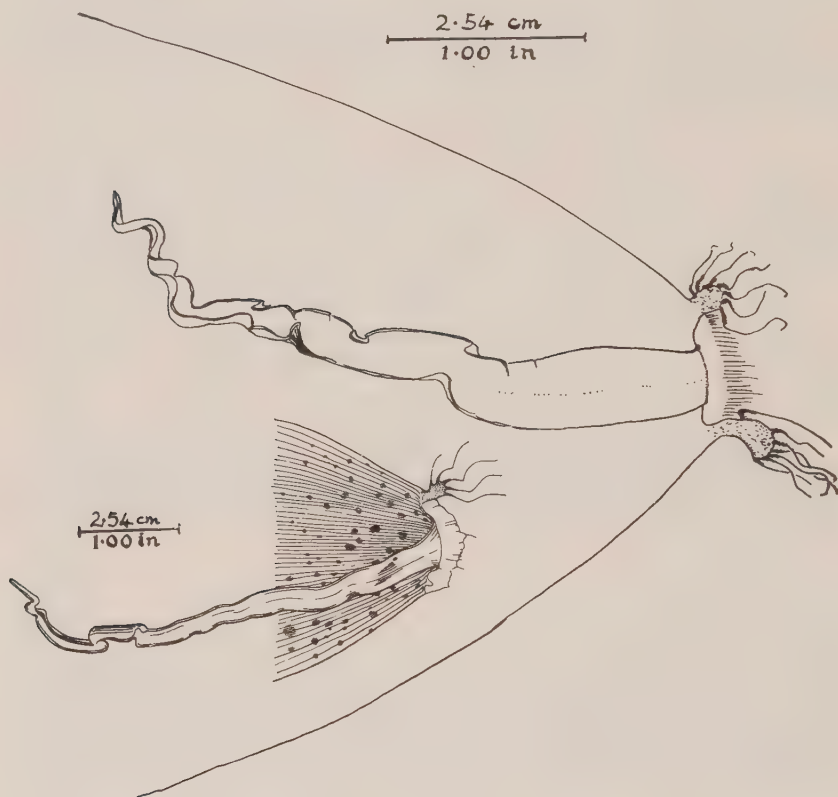


FIG. 3. *Phyllostachys elegans* McClure sp. nov. Outer aspect of apex of a mid-culm sheath: above, intact specimen; below, specimen showing but one well-developed auricle and a ligule from which most of the marginal bristles have been lost.

The type colony of this bamboo was developed from propagating material secured at Ta Ts'it, near Hung Mo Mt., Tan District, Hainan Island, China, sent by the writer to the U. S. Department of Agriculture in 1938. The local Chinese (Cantonese) name *Fa Chuk* (Flowered or Embroidered Bamboo) alludes to the conspicuous maculation of the culm sheaths. An earlier introduction, representing what appears to be a somewhat less vigorous strain of the species, is P. I. 110511, secured by the

writer at Mung Haang, Ts'ing-yuen District, Kwangtung province, China, and sent to the U. S. Department of Agriculture in 1936.

This species resembles *Ph. viridi-glaucescens* A. & C. Riv. in the appearance and variability of its culm sheaths; those of *Ph. elegans*, however, show a distinctly shorter ligule. Plants of these two species show little similarity in general appearance and *Ph. elegans* may be distinguished readily in the field by the more strongly tapered culms, the marked striation of the internode surface, and the visibly shorter internodes in the lower part of the culms. The leaf blades of the new species are smaller (shorter but proportionately broader) than those of *Ph. viridi-glaucescens*, and, in contrast with the latter, distinctly puberulent throughout the lower surface. The Chinese (Cantonese) vernacular name used in Mung Haang — *Man Sun* or *Man Chuk* (Elegant Shoot or Elegant Bamboo) — is the basis of the specific epithet.

***Phyllostachys glauca* McClure sp. nov.**

FIG. 4

Culmi usque et ultra 10 m. alti et 4 cm. diametro; *internodia* viridia, omnino glabra, delapsis tegentibus vaginis primo pulvere albo pulchre pruinosa, haud striata, usque et ultra 40 cm. longa (in culmo 10.22 m. alto, ut exemplo electo, internodio quarto decimo maximo longitudine) recta vel rarissime supra basin nonnulla leviter anfracta; *nodi* pulvino cicatriceque modice et subaequaliter eminentes, cicatrice glabra. *Culmi vaginae* ad apicem angustum truncatum sensim rotundatae vel angustatae dorso glabrae, ubique virides cum vino plus minusve valde suffusae, maculis fuscis (praesertim in basi apiceque) parce maculatae, raro paene immaculatae; *auriculae setae oralesque* raro evolutae; *ligula* fusca, lata et comparate brevis, apice truncata vel leviter undulata, raro (infimae tantum) concava, margine ciliata raro (praesertim superiores) invalide fimbriata; *vaginarum laminae* lanceolatae usque ad lineari-lanceolatae in apice hebet acuto subito angustatae, planae vel leviter naviculiformes, inferiores reflexae superiores patentes. *Foliorum vaginae* plerumque haud auriculatae; *ligula* valde evoluta primo saepius leviter purpureo-tincta; *foliorum laminae* subtus primiter secundum costam parce pilosae alibi subglabrae vel glabrescentes. *Inflorescentia* desunt.

Type in U. S. National Herbarium, Nos. 2177865–6 (2 sheets), collected by *F. A. McClure* (No. 21803), April 24, 1955 at the U. S. Barbour Lathrop Plant Introduction Garden where the plant is cultivated under P. I. 77011. The description is based on the plants in a colony about 27 years old.

Rhizomes of this species, from a garden in Nanking, Kiangsi province, China, were sent to the U. S. Department of Agriculture by the writer in 1926. They gave rise to rooted plants that survived quarantine and ultimately became established as P. I. 77011 at the U. S. Barbour Lathrop Plant Introduction Garden.

The specific epithet alludes to the distinctive misty green color of the young culms which is due to their evenly distributed overall covering of white powder. By this character this bamboo can readily be recognized in the field, even at a considerable distance.

This species is very similar to *Ph. flexuosa* in many respects. The ligules of the culm sheaths in *Ph. glauca* are broader and shorter in proportion, and fringed on the margin with minute cilia rather than bristles; they are somewhat more durable (less fragile) on drying. The blades of the culm

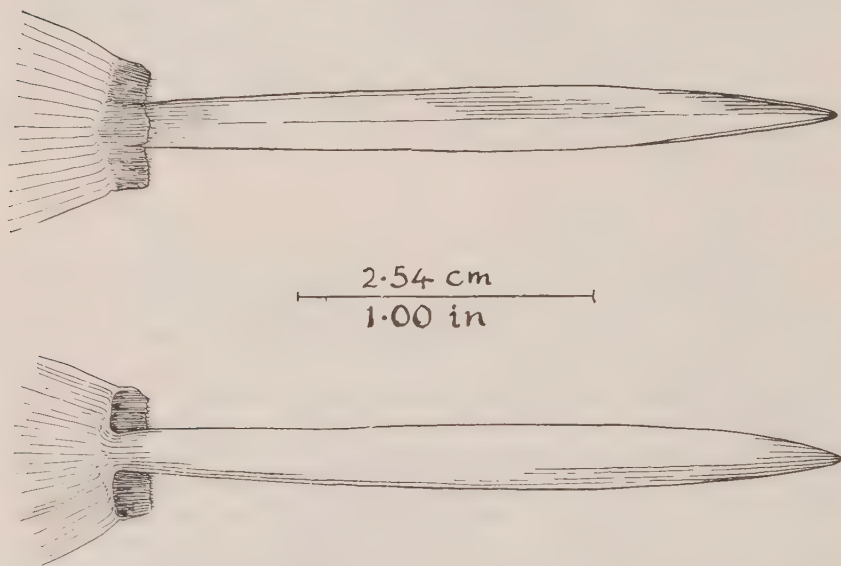


FIG. 4. *Phyllostachys glauca* McClure sp. nov. Inner (above) and outer aspects of a mid-culm sheath.

sheaths (particularly in the lower half of the culm) are appreciably broader in proportion to their length, and more abruptly narrowed at the tip than those of *Ph. flexuosa*. The culm sheaths in *Ph. glauca* are appreciably thicker and tougher in texture, and generally show fewer and more discrete dark spots than those of *Ph. flexuosa*. Plants of *Ph. glauca* (P. I. 77011) show greater vigor and larger ultimate stature than those of *Ph. flexuosa* (P. I. 52686 and 116965) under apparently identical growing conditions.

NOMENCLATURAL NOTES

Because of faulty original documentation, several of the names currently used for entities in the genus *Phyllostachys* are in need of critical examination. Among these are the following:

Phyllostachys edulis (Carr.) H. de Leh. (Houzeau de Lehaie is referred to hereinafter also as Houzeau). See discussion under *Ph. pubescens*.
Phyllostachys mitis A. & C. Riv. See discussion under *Ph. viridis*.

Phyllostachys reticulata (Rupr.) C. Koch. See discussion under *Ph. bambusoides*.

Phyllostachys sulphurea var. *viridis* R. A. Young. See discussion under *Ph. viridis*.

Phyllostachys bambusoides S. & Z., K. Bayer. Akad. Wiss. Abh. 3: 746, pl. 5, fig. 3. 1843. (Type species of the genus; based on a flowering specimen)

? *Bambusa reticulata* Rupr., St. Petersburg. Acad. Mem. VI Sci. Nat. 3: 148. 1839. (Based on a sterile leafy specimen); *Phyllostachys reticulata* (Rupr.) C. Koch., Dendr. 2(2): 356. 1873.

Madake of Japanese gardens.

From available evidence there appear to be grounds for reasonable doubt that Ruprecht's species is the same as *Phyllostachys bambusoides* S. & Z., the Chinese bamboo known universally in Japanese gardens as *Madake*. If the problem involved only the matter of priority, *Ph. reticulata* (Rupr.) C. Koch would clearly be the correct name for this bamboo. However, the identity of the type of *Bambusa reticulata* Rupr., which is the basis of *Ph. reticulata*, has not been clearly established. So the taxonomist is still confronted with the question, is it the *Madake* of Japanese gardens, or is it something else?

Let us consider the evidence, beginning with Ruprecht's description and notes (loc. cit.)

"59. *B. reticulata* n. sp. Culmi ramulis foliiferis dense fasciculatis, laevigatis, nitidis, nodis biannulatis parum tumentibus; vaginis inferioribus aphyllis, superioribus foliolo brevissimo sub 2 lineali appendiculatis, supremis 4-5 foliiferis, omnibus striato-sulcatis, vix compressis, glabris, margine subciliatis, ore fimbriatis, fimbriis mox evanescentibus; foliis lineari-lanceolatis (6-8: 48-70) acuminatis, basi in petiolum longiusculum (sub 2 lin.) attenuatis, firmis, pergamenis, glaberri-mis, supra striatis, subplicatis, subtus glaucescenti-cinereis.

V. sp. japonica (veros. c. Nangasaki lecta): Langsdorf!

"Ad ramulos (juniores ?) nunc descriptos haud cum dubio pertinent folia, omnibus proprietatibus descriptis similia, sed omni dimensione *majora*, pedalia et ultra, 2-3 poll. *lata*, inferiora magis ovata, latiora, superiora lanceolata, petiolo 6 lin. ad insertionem articulato, tumido, 2 lin. lato; lamina basi inaequaliter, secus costam mediam subtus valde prominulam ad latus magis evolutum, imprimis basi breve puberulo-tomentosa; nervis in q.l. 14 primariis, secundariis 9-11 venulis transversis (ut supra) creberrimis, anastomosantibus, inde parenchyma in *quadrotula minima* supra et subtus dispartientibus. (*B. reticulata*.)"

The last paragraph of the description, a very long one consisting of numerous references and many quotations from existing literature, has been omitted here for economy of space, since it sheds no light on the question under consideration.

Let us first direct our attention to the formal description (the first paragraph) ostensibly based on Langsdorf's specimen cited immediately

thereafter. "Culmi ramulis foliiferis *dense fasciculatis*" describes a character not found in any known species of *Phyllostachys*. Again, the statement "vaginis inferioribus aphyllis, superioribus foliolo brevissimo sub 2 lineali appendiculatis, supremis 4-5 foliiferis" is based on a condition that would not be found in any known species of *Phyllostachys* since in this genus the branch sheaths are promptly deciduous and fall away progressively as the leaf blades develop.

It requires no further analysis to make it clear that Ruprecht's description includes characters from at least one genus other than *Phyllostachys*. It cannot, therefore, be relied upon to clarify the specific identity of his type specimen if the specimen actually is a species of *Phyllostachys*.

But what of the type specimen itself? Immediately after the formal description Ruprecht cites a single specimen in words that, freely translated, say, "I have seen a Langsdorf specimen from Japan (apparently collected near Nagasaki)." The writer has not seen this specimen, but it presumably is still extant, along with the other material Ruprecht had before him, judging from the statements in the paragraph that follows the formal description. The type apparently consists of a sterile leafy branching specimen. No mention is made of flowers.

It is perfectly feasible to describe and identify bamboos on the basis of sterile vegetative material alone, *given adequate specimens of the critical structures*. It is only rarely, however, and in special cases, that a positive identification of a bamboo, or the differentiation of two closely related species, can be made on the basis of *sterile leafy branches alone*. That Koch, who transferred the specific epithet "reticulata" from *Bambusa* to the genus *Phyllostachys*, had an entirely erroneous idea of the nature of the latter genus is apparent from his comments that accompany the transfer (op. cit., p. 356-357).

Granted, however, for the sake of exploring the possibilities, that the Langsdorf specimen (Ruprecht's type) may represent a species of *Phyllostachys* (a group in which the *generic* determination can be made with confidence on the basis of adequate specimens of leafy branches) the specimen in question may be expected to represent one of the four species of that genus (all of Chinese origin) known to have been established in cultivation in Japan since early times. If the texture and dimensions of the leaves attributed to the specimen by Ruprecht in his diagnostic description are taken at face value, *Ph. pubescens* and *Ph. nigra* (including its forms) are ruled out, leaving *Ph. bambusoides* and *Ph. aurea* as possibilities. Here a critical complication arises. *Phyllostachys bambusoides* and *Ph. aurea* have very similar foliage. In recognition of this and other similarities (particularly in the inflorescence) of these two bamboos, Makino (Bot. Mag. Tokyo 11: 158, 1897) made the latter a variety of the former. Ohki, who made an exhaustive study of the systematic importance of spodiograms in the leaves of Japanese bamboos (Tokyo. Univ. Fac. Sci. J. Sec. III Bot. 4: 1-130, 43 figs. 1932) does not undertake to differentiate these two species by his method. However, to the writer, they are easily distinguishable by their culm sheaths and culm characters as well

as by their inflorescences. The writer considers them to be quite distinct species even though he is not able to separate them with confidence on the basis of sterile leafy branches alone.

The "reasonable doubt" mentioned at the beginning of this discussion focuses itself on the question, "Does the Langsdorf specimen, the type of *Bambusa reticulata* Rupr., represent the *Madake* of Japanese gardens, i.e. the plant known as *Phyllostachys bambusoides*, or is it something else?" The foregoing appeal to the available evidence leaves this question still unanswered. The reasonable doubt that clouds our view can be dispelled only by a positive identification of the Langsdorf specimen (connecting it with a known entity), supported by mention of one or more taxonomic characters by which it differs from comparable specimens of the other species with which it might be confused.

Current usage in Japan preponderantly favors the name *Ph. reticulata* (Rupr.) C. Koch for *Madake*, although Japanese taxonomists have offered no satisfactory documentation of their identification of Ruprecht's type. The preponderance of usage in Europe and the United States generally has favored the name *Phyllostachys bambusoides* for *Madake*. Until the type of *Bambusa reticulata* Rupr. can be shown to be unmistakably identical with this species, the writer can see no reason for displacing the well-founded name *Phyllostachys bambusoides* S. & Z. with the very inadequately documented *Ph. reticulata* (Rupr.) Koch.

The typical form of *Ph. bambusoides* is represented at the U. S. Barbour Lathrop Plant Introduction Garden by plants under P. I. 40842. This introduction is doubtfully reported (USDA Inventory of Seeds and Plants Imported, p. 89, *pl. vi.* 1915) to have reached this country via India, in 1890. Other introductions representing this typical form of the species are P. I. 12180 and 128787.

Phyllostachys pubescens Mazel ex H. de Leh., *Bambou*, p. 7 (Jan.) 1906; Nakai, *J. Jap. Bot.* 9: 27-29, *pl.* 6. 1933 (excl. syn.)

Phyllostachys edulis H. de Leh., *Bambou*, p. 39 (Jan.) 1906. (not ? *Bambusa edulis* Carr., *Rev. Hort.* 37: 380. 1866.)

Mosochiku of Japanese gardens.

TYPE: None cited. Neotype in U. S. National Herbarium, Nos. 2177859-60 (2 sheets), collected by F. A. McClure (No. 21800) April 17, 1955, from a colony cultivated under P. I. 80034 at the U. S. Barbour Lathrop Plant Introduction Garden.

Origin: China; introduced into Japan about 1737. (Satow, E. *Asiat. Soc. Japan. Trans.* 27(3): 35. 1899) ". . . In Europe it was confined until 1904 to the garden of the late M. Mazel at Prafrance, where it arrived around 1880, after the visit of the late M. Riviere." (H. de Leh. *op. cit.* p. 39)

In the United States the name *Phyllostachys edulis* (Carr.) H. de Leh.,

based on *Bambusa edulis* Carr., has generally been used for this plant. A translation of the original French description (Carr. loc. cit.) follows:

"*Bambusa edulis*; *B. mitis* hort. This species, the young shoots of which are said to be eaten as are those of hops, is a native of China. It is very vigorous and very hardy and belongs to the group *nudicaules*. Its characteristics follow:

"Stems erect, much branched, green. Bud sheath very large, soon becoming yellow; sheaths ciliate blackish, prolonged a little beyond the point of origin of the leaf blade. Leaves slender, very finely serrulate and almost ciliate on the margin, of a clear green above, glaucescent beneath, very long-acuminate at the apex."

Carriere left no type and supplied no illustration of this bamboo. From his very generalized and incomplete description one cannot, without making bold and unfounded assumptions, guess even the generic affinity of his bamboo, let alone its specific identity. The character "much branched" ascribed by Carriere to his plant excludes it from the genus *Phyllostachys* where the branches are paired at each node.

Houzeau's statement about the date of the first introduction of *Phyllostachys pubescens* into France by Mazel in about 1880 (op. cit. p. 9; see also quotation above in the paragraph beginning "Origin:") makes it extremely unlikely that this species was available to Carriere in 1866. The possibility that he may have had plants of it that originated from propagules of the heterocyclic form discussed below has been considered. However, this possibility also shrinks to extreme improbability when we consider the evidence.

Carriere did not describe *Bambusa heterocycla* until 1878, twelve years after he described *B. edulis*. If both the species and the heterocyclic form had presented themselves to his attention either simultaneously or contemporaneously, he would almost certainly have focused on the heterocyclic form first. His conspicuous record (Rev. Hort. passim) for bringing horticultural novelties to light in advance of their having been described by taxonomists supports this view. In any case, the original application of the name *Bambusa edulis* still remains uncertain.

In January, 1906, Houzeau (op. cit., p. 38) discovered that Japanese botanists had been applying the name *Phyllostachys mitis* A. & C. Riv. to the *mosochiku* of Japan, and that Makino's description of it (Makino, T., Bot. Mag. Tokyo 15: 68. 1901) corresponded perfectly to the bamboo Houzeau himself had just described as *Ph. pubescens* Mazel (op. cit. p. 7). This discovery lead Houzeau to prepare an article, "Les deux *Phyllostachys mitis*" (op. cit. p. 38-39) in which he presented pertinent facts and made an adjustment in the nomenclature that he deemed appropriate. He was in a position to do this since he had in his collection living plants of the two bamboos involved; the true *Ph. mitis* A. & C. Riv., and the controversial *mosochiku* of Japan. The point of present concern is that Houzeau abandoned the name *Ph. pubescens* Mazel which he had just set up for the *mosochiku*, and substituted for it the new combination *Ph. edulis* (Carr.) H. de Leh.

An attempt is made in the following lines to reconstruct the mental process by which Houzeau was led to do this in the face of the demonstrated uncertainty of the application of Carriere's name.

Probably upon recognizing his *Ph. pubescens* in Makino's description under the name *Ph. mitis* he first re-read the Rivieres' description of *Ph. mitis*. Here he saw the synonym [*Bambusa*] *edulis* given. Although no authority was cited by the Rivieres for the name *edulis*, Houzeau probably was led to look up the original description of *Bambusa edulis* by Carriere. (He may have been influenced in this by the fact that Makino (loc. cit.) had given *Bambusa edulis* Carr. in his synonymy.) Carriere gives *B. mitis* as a synonym for his *B. edulis*. The psychological impact of this reciprocal citation of synonymy seems to have convinced Houzeau that he had discovered the reason why the two bamboos in question had become confused in the minds of the Japanese botanists. He seems to have been drawn irresistibly to the perfectly apparent solution: "If one of the two confused bamboos (both of which he had growing in his garden) is *Phyllostachys mitis* the other must be made *Phyllostachys edulis*!" He put this idea into effect at once. Unfortunately, in doing so he overlooked the implications of the fact he recorded earlier in the same article relating to the first introduction of *Ph. pubescens* into France about 1880 (*vide supra*). Evidently, however, he soon realized that his action in changing the name had been hasty, for he promptly reverted (op. cit. p. 55 et seq.) to the use of the name *pubescens* for the plant he had temporarily called *Ph. edulis*. This retreat from the use of the name *edulis* and the subsequent concurrence of Japanese usage are significant testimony to the fact that the application (content) of the name *edulis* is not satisfactorily documented, and still remains obscure.

In the light of the foregoing account, it is of interest to turn attention at this point to the fact that Lindley (Penny Cyclop. 3: 357. 1835) described, under the name *Bambusa pubescens* Loddiges, a bamboo "obtained by the English from the collections of France." The writer has examined a photograph of the type of *Bambusa pubescens* Loddiges ex Lindl. which is preserved in the University Herbarium, Cambridge, England. The specimen is only a sterile leafy twig but it is possible to assert with confidence that it clearly is not a species of *Phyllostachys* and so has nothing to do with *Ph. pubescens* Mazel ex H. de Leh.

Article 75 of the International Rules of Botanical Nomenclature (1952) reads as follows: "A name of a taxon must be rejected if it is used with different meanings and so becomes a long-persistent source of error." In the sense of Article 75 the combination *Phyllostachys edulis* and the name *Bambusa edulis* on which it is based appear to be *nomina rejicienda*.

A bizarre form of this species, the tortoise-shell bamboo, or *kikkuchiku* of Japan, known as the Lohan Chu in China, has been given taxonomic status as *Bambusa heterocycla* Carr., *Phyllostachys edulis* var. *heterocycla* (Carr.) H. de Leh., *Ph. pubescens* var. *heterocycla* H. de Leh. etc. Being based on a "monstrosity," however, these names must all be rejected. (Internatl. Rules Bot. Nomencl. Art. 77. 1952)

Phyllostachys viridis (Young) McClure comb. nov.

Phyllostachys sulphurea var. *viridis* R. A. Young, Wash. Acad. Sci. J. 37: 345. 1937.

Phyllostachys mitis A. & C. Riv. Soc. Acclim. B. Ser. III 5: 689. 1878, quoad descriptionem tantum; haud *Bambusa mitis* Poir. necque *Arundo mitis* Lour.

TYPE: “. . . deposited in the U. S. National Herbarium, nos. 1682470 and 1682471, collected in Plant Introduction Garden, Savannah, Ga., January 11, 1937, by D. A. Bisset; grown from material obtained in 1928 from Gaston Negre, Generargues, France, under the name *Phyllostachys mitis*.” (Young, loc. cit.) This species is represented at the U. S. Barbour Lathrop Plant Introduction Garden by the original colony under P. I. 77257.

Origin: “China; introduced [into France] in 1840 by M. de Juncigny and in 1855 or 1856 by M. Montigny, French Consul at Shanghai, who is said to have imported it from Cochinchina.” (Houzeau de Lehaie, Bambou, p. 39, 1906. Notes on *Phyllostachys mitis* A. & C. Riv. in an article entitled “Les deux *Phyllostachys mitis*.”)

The above-mentioned reference to Cochinchina as a source of Montigny's plants probably is not well-founded, as no documented record of the occurrence of the species in Cochinchina has come to light. However, this reference to Cochinchina may have been what led the Rivières to take up the name *Arundo mitis* Lour. (Fl. Cochin. p. 57. 1790). On the basis of material collected in Annam by Dodo and Parrant, E. D. Merrill (Amer. Phil. Soc. Trans. 24(2): 85. 1935) identifies *Arundo mitis* Lour. as a species of *Dendrocalamus*.

The name *Phyllostachys sulphurea* var. *viridis* Young is untenable because the name *Ph. sulphurea* belongs to a specifically distinct plant. The latter is treated elsewhere in this paper under *Ph. bambusoides* cultivar ALLGOLD (P. I. 89701). The plant (represented by P. I. 89718) misidentified by Houzeau (Bambou p. 99 et passim. 1906) as *Ph. sulphurea* becomes cultivar. ROBERT YOUNG of *Ph. viridis* (see p. 195).

HORTICULTURAL FORMS

The following entities that have heretofore been given taxonomic status as varieties or forms appear to belong in a more informal category, to which the term “cultivar” is applicable.

Phyllostachys bambusoides S. & Z.

CULTIVAR: CASTILLON

Reference to this entity will be found in the literature under the following botanical names: *Bambusa castilloni* Marliac ex Carr. Rev. Hort., 58: 513. 1896. *Phyllostachys castillonis* (Marl.) Mitf., Garden 47: 3. 1895. *Ph. bambusoides* var. *castillonis* Makino, Bot. Mag. Tokyo 14: 63. 1900. *Ph. quilioi* var. *castillonis* H. de Leh., Bambou, p. 29. 1906. *Ph. nigra* var.

castillonis (Mitf.) Bean, Kew Bull., p. 232. 1907. *Ph. reticulata* var. *castillonis* (Marl.) Makino, Bot. Mag. Tokyo 26: 21. 1912.

The CASTILLON bamboo is distinguished from the typical form of the species by the color pattern of the culms, culm sheaths, and leaves, as follows: Ground color of culm internodes (and branches) bright golden yellow (sometimes suffused with dilute wine in the lower part of the culm); the internodes of culms and branches show a broad green panel on the groove above each bud or branch insertion (and in analogous positions where buds or branches do not occur); culm sheaths have a greenish yellow background and a few green stripes. Occasional leaf blades show cream stripes. The ultimate culm size of this form is considerably less than that of the typical form of the species. CASTILLON differs from ALLGOLD principally in having the sulcus of the culm internodes green, and in having green striping always present outside the sulcus.

The colony of CASTILLON (P. I. 42659) under cultivation at the U. S. Barbour Lathrop Plant Introduction Garden is derived from plants purchased from the Yokohama Nursery Company, Japan, in 1916.

"This form is native to China. . . . It was introduced into Japan in the early days" (Nakai, T., J. Jap. Bot. 9: 240. 1933. Transl. Katsura, ed. R. A. Young. 1936). By 1886 it was established in cultivation in France (teste Carriere, loc. cit.). Tsuboi says that he found a culm of this bamboo (as a spontaneous mutation) in a forest of *Phyllostachys bambusoides* in Yawata-Mura, Gifu-ken, Japan (Illus. Jap. sp. Bamb. ed. 2, p. 6, 1916. Transl. Katsura, ed. R. A. Young. 1935).

CULTIVAR: ALLGOLD.

References to this entity will be found in the literature under the following botanical names: *Bambusa sulphurea* Carr., Rev. Hort. 45: 379. 1873. *Phyllostachys sulphurea* A. & C. Riv., Soc. Acclim. B. Ser. 3, 5: 773. 1878. *Ph. castillonis* var. *holochrysa* Pfitz., Deut. Dendr. Ges. Mit. 14: 60. 1905. *Ph. quilioi* var. *castillonis holochrysa* Regel ex H. de Leh., Bambou, p. 118. 1908. *Ph. bambusoides* var. *castilloni holochrysa* (Pfitz.) H. de Leh., Congr. Internat. de Bot. 3. Actes 2: 228. 1912. *Ph. reticulata* var. *sulphurea* Makino, Bot. Mag. Tokyo 26: 24. 1912. *Ph. bambusoides* var. *sulphurea* Makino ex Tsuboi, Illus. Jap. Sp. Bamb. ed. 2, p. 7, pl. 5. 1916. *Ph. reticulata* var. *holochrysa* (Pfitz.) Nakai, J. Jap. Bot. 9: 34. 1933.

ALLGOLD differs from the CASTILLON Bamboo in lacking the green panel on the sulcus of culm and branch internodes, and in having the green striping otherwise *very sparse, often lacking entirely*. The purely golden phase is the one illustrated by Tsuboi (loc. cit.). It is believed to be the one Carriere had before him when he described *Bambusa sulphurea* (loc. cit.) since he makes no reference to green stripes. Tsuboi (loc. cit.) mentions a plant of *Phyllostachys bambusoides* var. *sulphurea* he had in his own garden, "segregated from the roots of Ginmeichiku" i. e. from the CASTILLON Bamboo. This fact is interesting, and may be significant in view of the circumstance that plants of the bamboo here named ALLGOLD,

purchased by the U. S. Department of Agriculture from V. N. Gauntlett in 1930, were received under the name *Ph. bambusoides* var. *castilloni*. They are growing at the U. S. Barbour Lathrop Plant Introduction Garden under P. I. 89701.

CULTIVAR: SLENDER CROOKSTEM.

References to this entity will be found in the literature under the following botanical names:

Phyllostachys bambusoides S. & Z., illustrated as an abnormal culm. Tsuboi, Illus. Jap. Sp. Bamb. ed. 2, pl. 58. 1916. *Ph. reticulata* forma *geniculata* Nakai, J. Jap. Bot. 9: 34. 1933. *Ph. bambusoides*. Variety Slender Crookstem. USDA. Some bamboos growing at the U. S. Barbour Lathrop Plant Introduction Garden, Savannah, Georgia. Mimeo. p. 7, 1947.

SLENDER CROOKSTEM is distinguished from the typical form of the species by the occurrence, in a high percentage of the culms, of a curve (sometimes compound) near the base. The culms are often more slender in relation to their height than those of the typical form of the species; the culm nodes are generally less salient. Buds are borne at a lower level on culms of comparable size, and frequently more of the lower buds remain dormant than in the culms of the typical form of the species. There is often a more copious development of hairs on the culm sheaths, and these often develop on sheaths of culms of smaller size than in the typical form of the species.

Nakai's bamboo, described as differing from the typical form of the species in having more slender culms, of which the lowest part is "always zigzag" in form, appears to be the same as SLENDER CROOKSTEM now growing at the U. S. Barbour Lathrop Plant Introduction Garden under P. I. 146420. The plants under this number came from rhizomes secured in Kwangtung province, China, and sent to the U. S. Department of Agriculture by the writer in 1925.

Phyllostachys nigra (Lodd.) Munro

CULTIVAR: HENON.

References to the HENON Bamboo will be found in the literature under the following botanical names:

Bambusa puberula Miq., Mus. Bot. Lugd. Batav. Ann. III, 2: 285. 1866. *Phyllostachys puberula* (Miq.) Munro, Gard. Chron. (n. s.) 6: 773. 1876. *Ph. henonis* Mitf., Garden 47: 3. 1895. *Ph. nigra* var. *henonis* (Mitf.) Stapf apud Rendle, Linn. Soc. Bot. 36: 443. 1904.

The HENON Bamboo is, in all probability, the "biological parent" of *Phyllostachys nigra* itself and of all the entities associated with it in the literature as taxonomic varieties or forms. However, since the black-stemmed one was the first to be named (*Bambusa nigra* Loddiges ex Lindl., Penny Cycloped. 3: 357. 1835) it becomes the "taxonomic species" now called *Phyllostachys nigra* (Lodd.) Munro. The others (including the

HENON Bamboo), since they do not differ from it, or among themselves, in any morphological characters whatsoever, are, therefore, properly treated under that name as cultivars.

The HENON Bamboo is represented at the U. S. Barbour Lathrop Plant Introduction Garden by plants under P. I. 24761, 66787, and 75158.

CULTIVAR: BORY.

References to the BORY Bamboo will be found in the literature under the following botanical names:

Phyllostachys boryana Mitf., Garden 47: 3. 1895. *Ph. puberula* var. *boryana* Makino, Bot. Mag. Tokyo 14: 64. 1900. *Ph. nigra henonis* forma *boryana* Makino, Bot. Mag. Tokyo 26: 26. 1912.

The BORY Bamboo differs from the HENON Bamboo solely in the slightly smaller ultimate size of the culms of the former, and in their development during the first year or so of a few scattered, irregularly shaped dark spots on the lower internodes. The BORY Bamboo has a larger mature culm and its spots are much larger and spaced much farther apart than those of the typical form of the species.

The BORY Bamboo is represented at the U. S. Barbour Lathrop Plant Introduction Garden by plants under P. I. 77258, purchased from Gaston Negre, Generargues, France, in 1928.

Phyllostachys viridis (Young) McClure

CULTIVAR: ROBERT YOUNG.

This spontaneous, apparently stable mutant, here named the ROBERT YOUNG Bamboo, differs from *Ph. viridis*, from which it originated, in having a smaller mature stature and a distinctive coloration. The culms and branches are at first sulphur-green, with darker green stripes on the lower internodes and a narrow dark green band immediately below each sheath scar. The sulphur-green background gradually turns to old gold and the green stripes persist. The culm sheaths are slightly paler than those of the species, and occasionally show a slender green stripe or two. Occasional leaf blades show cream stripes.

The ROBERT YOUNG Bamboo is in cultivation at the U. S. Barbour Lathrop Plant Introduction Garden under P. I. 89718. Plants of it were received by the U. S. Department of Agriculture from V. N. Gauntlett & Co., Chiddingfold, Surrey, England, in 1930. No record of its introduction into Europe has been found. It could have appeared there, *de novo*, as a mutation from the species, whose introduction is recorded. The stock from which the Gauntlett plants came probably originated as a spontaneous variation in one of the introductions of the parent species from China. The ROBERT YOUNG Bamboo has been observed to originate spontaneously (personal observation, May, 1955) from propagating material of *Ph. viridis* in the nursery at the U. S. Barbour Lathrop Plant Introduction Garden.

Houzeau (Bambou, p. 57, 99. 1906) identified this bamboo as *Phyllostachys sulphurea* A. & C. Riv. On the strength of this identification Houzeau (op. cit. p. 214, pl. 8. 1907) made *Ph. sulphurea* a variety of *Ph. mitis* (= *Ph. viridis* [Young] McClure). His plant (here named ROBERT YOUNG Bamboo) is indeed a form of that species. However, the name "sulphurea" was misapplied by him. As pointed out by R. A. Young (Wash. Acad. Sci. J. 37: 344. 1937) the Rivières give *Bambusa sulphurea* Hort. (a name without standing) instead of *B. sulphurea* Carr., as a synonym of *Ph. sulphurea* A. & C. Riv. This may have been an inadvertency. In any case a comparison of the Rivières' description of *Ph. sulphurea* with Carrière's description of *Bambusa sulphurea* strongly suggests that the Rivières correctly believed they had the same plant that Carrière had.

The writer sees no reason for following Houzeau's interpretation of *Ph. sulphurea* since the original description of it does not apply to the plant he had. The material received by the U. S. Department of Agriculture under the name *Phyllostachys sulphurea* from Gauntlett is growing at the Barbour Lathrop Garden under P. I. 89718. Neither the description of *Bambusa sulphurea* Carr. nor that of *Phyllostachys sulphurea* A. & C. Riv. makes any reference to green stripes, though these are found on every culm of the ROBERT YOUNG Bamboo. However, both descriptions apply perfectly to the bamboo treated by Japanese botanists as a variant of *Phyllostachys bambusoides* S. & Z., and by the writer as a horticultural form of that species (see Cultivar ALLGOLD, p. 193 of this paper).

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